Biological Report 85(7.20)
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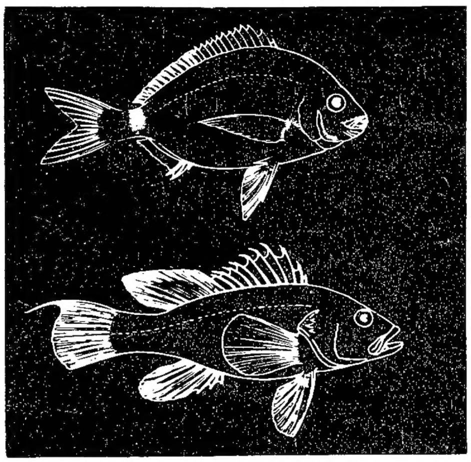

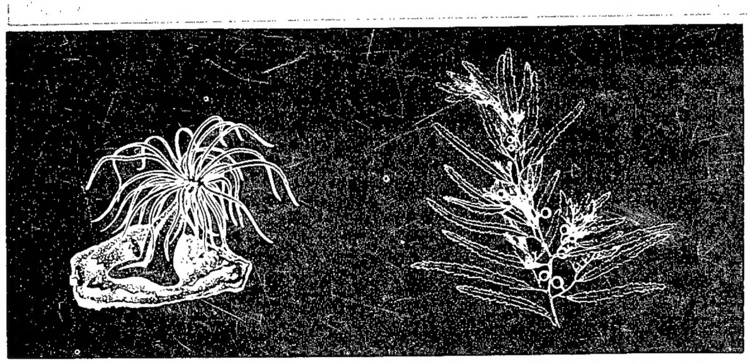

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
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Cover:

Fish (top left), anemones (top center), and seaweeds (top right) are common organisms associated with rubble structures such as the jetties at Murrells Inlet, South Carolina (bottom photograph).

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THE ECOLOGY OF RUBBLE STRUCTURES OF THE SOUTH ATLANTIC BIGHT: A COMMUNITY PROFILE

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U.S. Department of the Interior
Fish and Wildlife Service
National Wetlands Research Center
Washington, DC 20240

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Library of Congress Cataloging-in-Publication Data

Hay, Mark E.
The ecology of rubble structures of the South Atlantic bight.

(Biological report ; 85-7.20)
"Performed for U.S. Department of the Interior, Fish and Wildlife Service, National Wetlands Research Center."
Bibliography: p.
Supt. of Docs. no.: I 49.89/2:85(7.20)
1. Marine ecology--South Atlantic Bight. 2. Biotic communities--South Atlantic Bight. I. Sutherland, John P. II. Watzin, Mary C. III. National Wetlands Research Center (U.S.) IV. Series: Biological report (Washington, D.C.) ; 85-7.20. V. Title.

QH93.9.S68H39 1988 574.5'2636 88-600381

Suggested citation:

Hay, M.E., and J.P. Sutherland. 1988. The ecology of rubble structures of the South Atlantic Bight: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.20). 67 pp.

PREFACE

This community profile provides an introduction to the ecology of communities on rubble structures in the South Atlantic Bight (Cape Hatteras, North Carolina, to Cape Canaveral, Florida). The most prominent rubble structures in this area are jetties built at the entrances to major harbors. We concentrate much of our discussion on these types of structures since most of the available literature concerns jetties or biological communities similar in species composition to those that occur on jetties. However, we also discuss the ecology of natural hard-substrate habitats in general and how these compare with the communities that develop on rubble structures. It is our hope that this text will serve as a general, yet thorough, review of why such structures are built, their general effects on near shore sediment dynamics, and what forces affect the organisms that live in close association with these structures.

After an initial discussion of the different types of rubble structures (Chapter 1) and the physical factors that affect the organisms associated with them (Chapter 2), we devote a major portion of our text to the ecology of rubble-structure habitats. In Chapter 3, we describe the community composition, distribution, seasonality, and recruitment patterns of the major types of organisms found on rubble structures (plankton, seaweeds, invertebrates, fishes, and birds). We also describe the major species within most of these groups and review some aspects of their basic natural history. In Chapter 4, we discuss the major physical and biological factors affecting the organization of intertidal communities, sunlit subtidal communities, and shaded subtidal communities. We also evaluate the potential effects of complex, and often indirect, interactions in structuring these communities. The effects of rubble structures on shoreline evolution and engineering are considered in the final chapter (Chapter 5) on management considerations.

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millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
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liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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ACKNOWLEDGMENTS

Order of authorship was decided by the flip of a coin.

Sections of this profile were reviewed by J.E. Duffy, P.F. Hay, S. Ortega, P.E. Renaud, and 5 anonymous reviewers. Illustrations were produced with the help of S. Ortega, H. Page, V. Page, P.E. Renaud, and S. Taylor. R. Forward provided the data for Figure 3. O. Pilkey, T. Clayton, and L. Taylor were especially helpful in providing data for Chapters 1 and 5. Information on invertebrates was provided by W. Nelson, W. Kirby-Smith, and R. Van Dolah. Information on birds was provided by C. Marsh, J. Parnell, and W. Hon. To all we are grateful.

The funding for this project was provided by the U.S. Army Corps of Engineers, Waterways Experiment Station.

CHAPTER 1. INTRODUCTION

The South Atlantic Bight borders the United States coastline from Cape Hatteras, NC, to Cape Canaveral, FL. The shoreline along the Bight is sandy and characterized by numerous barrier islands separated by tidal inlets. Interspersed along this coastline, especially at inlets, are various artificial structures composed of hard rubble materials. These rubble structures are the focus of this profile.

1.1 DEFINITION OF RUBBLE STRUCTURES

Rubble structures are mounds of random-shaped and random-placed stones protected with a cover layer of selected stones or specially shaped concrete armor units (Whalin et al. 1984). Most commonly they are constructed of large boulders, but they can be built from a wide variety of materials, including steel, concrete, pilings, wood timbers, and plastic bags filled with sand (Whalin et al. 1984). Rubble structures can be divided into two general categories based upon their position relative to the shoreline and their purpose. The first category includes those structures built perpendicular to the shoreline and designed to interrupt the littoral transport of sediment. This category includes jetties, weir jetties, and groins. The second category of rubble structures includes those built parallel to the shoreline and designed to prevent waves from reaching the higher elevations of the beach. This category includes breakwaters, seawalls, bulkheads, and revetments.

Structures Perpendicular to the Shoreline

Jetties are structures used at inlets to stabilize the position of the navigation channel, to shield vessels from wave forces, and to control the movement of sand along the adjacent beaches so as to minimize the movement of sand into the channel.

Weir jetties are updrift jetties with a low section or weir. Littoral drift moves over the weir section into a predredged deposition basin which is dredged periodically.

Groins are shore protection structures built to trap littoral drift or retard erosion of the shore. They are usually shorter than jetties and are used along the beach away from inlets.

Structures Parallel to the Shoreline

Breakwaters are wave energy barriers designed to protect any landform or water area behind them from the direct assault of waves.

Seawalls are structures separating land and water areas, primarily designed to prevent erosion and other damage due to wave action. Seawalls are designed to receive the impact of the sea at least once during each tidal cycle.

Bulkheads are structures built higher on the shore than a seawall or a revetment to retain or prevent sliding of the land. A secondary purpose is to protect the upland against damage from wave action during storms.

Revetments are facings of stone, concrete or wood built to protect a scarp, embankment, or shore structure against erosion by wave action or currents. Revetments are a protective armor, rather than a retaining structure.

1.2 RUBBLE STRUCTURES OF THE SOUTH ATLANTIC BIGHT

Although many small rubble structures exist throughout the South Atlantic bight, the most prominent rubble structures in this area are the jetties constructed to protect the entrances to the region's major harbors (Figures 1 and 2). Some of the largest jetties are described below.

Beaufort, North Carolina

There are two small jetties near Beaufort Inlet. Radio Island jetty was built prior to 1939 (C.G. Bookhout, Duke University Marine Laboratory; pers. comm.) to prevent the shoaling of Bulkhead Channel leading to Beaufort Harbor. Early surveys (U.S. Coast Survey Chart No. 874, 1874; U.S. Coast and Geodetic Survey No. 3387, 1913) suggest that Shackleford jetty was constructed near the turn of the century in an early attempt to stabilize Beaufort Inlet. Neither of these jetties is currently more than 300 m in length. Although small, their location near the Duke University Marine Laboratory and the Institute of Marine Sciences of the University of North Carolina at Chapel Hill has made them among the best studied jetties in the South Atlantic Bight. For this reason they are included here.

Masonboro Inlet, North Carolina

This inlet is between Wrightsville Beach to the north and Masonboro Island to the south. The north jetty off Wrightsville Beach is 1,140 m long and was constructed in 1965-1966 (Kieslich 1981). The continued transport of sand into the

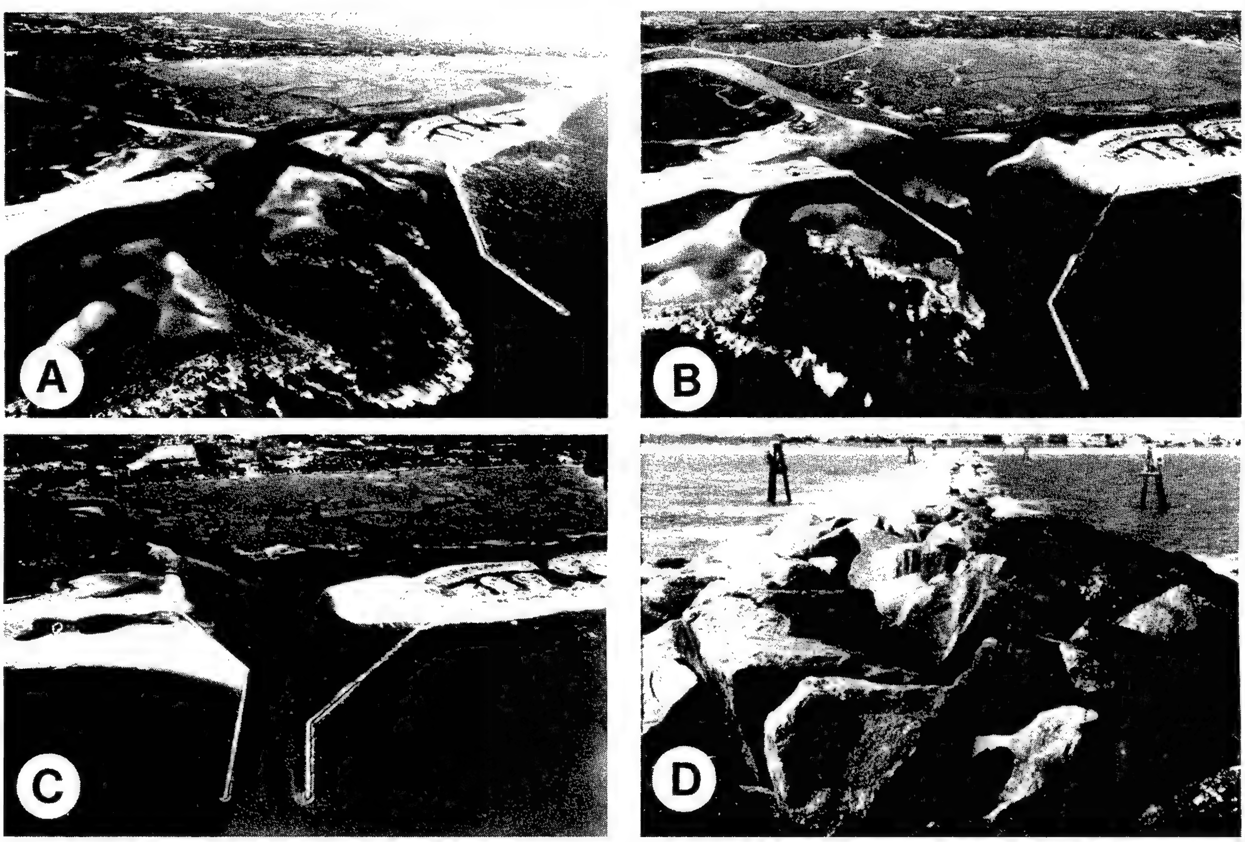


Figure 1. The jetties at Murrells Inlet, SC, in various stages of construction (A and B) and completed (C). (D) shows a close-up of the large boulders used to form oceanic jetties (photos courtesy of U.S. Army Corps of Engineers).

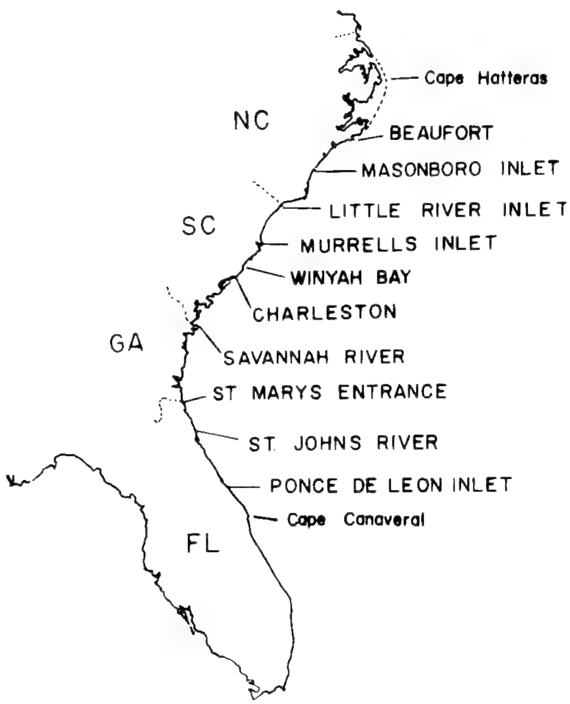


Figure 2. Major jetties in the South Atlantic Bight.

channel from the south necessitated the construction of a southern jetty off Masonboro Beach in 1979-1980. The southern jetty is 560 m long (Whalin et al. 1984).

Little River Inlet, between North and South Carolina

Two jetties, both approximately 1,090 m in length, were constructed between 1981 and 1983 (Hansen and Ward 1986). They are designed to protect the channel between Bird Island to the north and Waites Island to the south.

Murrells Inlet, South Carolina

The north jetty extends some 1,040 m off Garden City Beach and was constructed between 1977 and 1979 (Van Dolah et al. 1984). The south jetty, off Huntington Beach, is approximately the same length and was constructed between 1979 and 1980.

Winyah Bay, South Carolina

Two jetties were constructed around the turn of the century at the entrance to Winyah Bay. A photograph in the office of Senator Bill Doar, Georgetown, SC, shows them under construction in 1898. The north jetty off North Island is some 1,938 m in length, while the south jetty off Sand Island is 4,060 m long.

Charleston, South Carolina

Construction on two jetties, 4,060 to 4,689 m in length, was completed in 1896 (Neal et al. 1984). Since that time Sullivans Island to the north has experienced a net accumulation of sand, while Morris Island to the south has suffered severe erosion.

Savannah River, Georgia

There are two jetties constructed between 1890 and 1898 that protect the Savannah River Harbor (Griffin and Henry 1982). These jetties extend seaward approximately 3,658 m and have interrupted littoral transport of sand to the south. This and continued dredging of the channel have resulted in considerable erosion on Tybee Island, located south of the Savannah River.

St. Marys Entrance, between Georgia and Florida

The entrance is bordered on the north by Cumberland Island and on the south by Amelia Island. Work began on the two jetties in 1881 and continued until they reached their present form in 1927 (Parchure 1982). The north jetty is 5,980 m long and the south jetty is 3,500 m in length. Since their construction, sand has accumulated on both the north and south sides of the entrance.

St. Johns River, Florida

The initial jetties were constructed between 1880 and 1895. The northern jetty extended 3,500 m seaward from Fort George Island. The southern jetty extended from Guano Island and was 2,650 m long. Work continued periodically until 1951 when the jetties attained lengths of 4,430 and 3,490 m, respectively (Pilkey et al. 1984). The jetties have interfered with the southward transport of sand and have caused severe erosion to the south of the inlet.

Ponce de Leon Inlet, Florida

The inlet lies between barrier islands on which are located Daytona Beach to the north and New Smyrna Beach to the south. Two jetties, approximately 1,250 m long, were built between 1968 and 1972 (Jones and Mehta 1978). Their construction has stabilized the inlet, but has apparently interrupted the northward movement of sediment. Beaches to the north have eroded while those to the south have experienced considerable accretion.

Natural System Counterparts

There are few natural counterparts to the hard substrate provided by open ocean jetties in the South Atlantic Bight. However, low relief rocky outcrops are found in the nearshore zone at a small area north of Cape Fear in North Carolina and along the northern half of the South Carolina coast. Rock outcrops also occur near Marineland in northern Florida (Stephenson and Stephenson 1972; Searles 1984). In sheltered waters, flora and fauna similar to those of artificial structures are found on submerged vegetation (Thayer et al. 1984; Keough and Chernoff 1987), oyster reefs (Wells 1961; Dame 1979) and shell rubble.

Other Artificial Structures

Similar organisms are also found on almost any hard substrate placed in the water, including pilings, docks, boats, and refuse such as cans and bottles. Indeed, the epifaunal fouling community is renowned for the trouble it causes when growing on human made structures, particularly boats. Much of what we know about the invertebrate community comes from studies conducted on artificial settling plates (e.g., Sutherland and Karlson 1977). There is no doubt that the activities of people in the South Atlantic Bight have increased the habitat space for these epibenthic organisms.

CHAPTER 2. PHYSICAL ENVIRONMENT

This chapter characterizes the physical environment of the South Atlantic Bight. The physical variables most important to rubble communities include the temperature and salinity of the water, and the amount of available light and nutrients. Water movement in the form of currents, tides, and waves is also important, particularly because of the way it affects sediment transport along the beach. In this chapter we consider each of these physical variables in turn.

2.1 TEMPERATURE AND SALINITY

The American Atlantic Temperate Region extends from Cape Cod, MA, to southern Florida (Gosner 1979). Cape Hatteras is a natural biogeographic boundary along the east coast dividing this region into the Virginian province in the north and the Carolinian province in the south. The southern boundary of the Carolinian province is Cape Canaveral. Thus, the Carolinian province coincides with the area treated in this profile.

Cape Hatteras and Cape Canaveral mark significant temperature transition zones. In the northern portion of the Carolinian province (North Carolina) water temperatures can exceed 30 ^{o}C in summer and drop to 0 ^{o}C in Winter (Sutherland and Karlson 1977; W. Kirby-Smith, Duke University Marine Laboratory; pers. comm.). As latitude decreases, winter temperatures especially are gradually ameliorated. In central Florida, water temperatures range from 30 ^{o}C in summer to 14 ^{o}C in winter (Mook 1980).

In this profile we restrict our attention to the outer coast and to the sounds and estuaries where the salinity generally remains above 20 ppt. The flora and fauna of these regions are basically marine.

2.2 LIGHT AND TURBIDITY

In the South Atlantic Bight, tides, waves, and wind-generated turbulence re-suspend bottom sediments in the shallow waters on the Continental Shelf. This sediment resuspension, combined with high estuarine and nearshore phytoplankton productivity, produces turbid inshore waters that drastically reduce light penetration. Reduced light penetration appears to be the major factor restricting plant growth to the shallow portions of most jetties. Figure 3 shows the relationship between irradiance and wavelength taken on the same day for different depths at an inshore site in Bogue Sound, NC (the turning basin at Morehead City), and a site approximately 6 km offshore from Bogue Sound. As can be seen, light decreases dramatically with depth in nearshore waters, where rubble structures are generally located.

2.3 NUTRIENTS

Nutrient conditions surrounding jetties are important because they affect the growth of the seaweeds attached to the jetties and the growth of phytoplankton in the overlying waters. These phytoplankton are consumed by benthic filter feeders on the jetties. On jetties subject to strong wave or tidal action, plants may be minimally affected by low nutrients because new water is constantly flowing by and because turbulence interrupts the formation of diffusion barriers around the seaweed thallus. Nitrogen is most

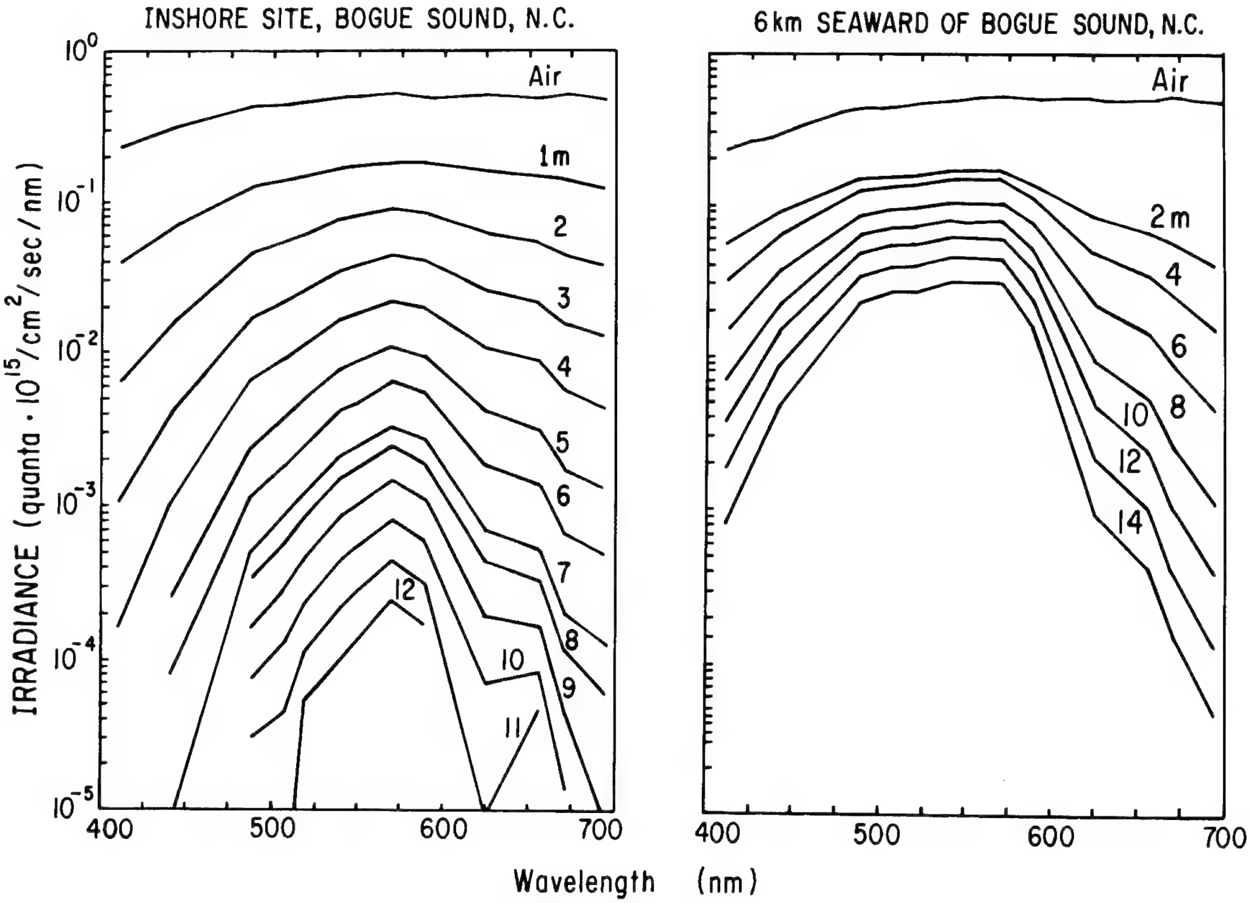


Figure 3. Irradiance versus wavelength for an inshore site (left) in Bogue Sound, NC, and for a site 6 km offshore (right). The numbers on each line indicate depth in meters. (Data provided by R. Forward, Duke University Marine Laboratory.)

commonly the nutrient limiting plant growth in coastal waters. In summers, the availability of dissolved inorganic nitrogen may change by more than an order of magnitude on a diel cycle, rising at night and falling dramatically during the day as it is consumed during photosynthesis (Litaker et al. 1987). Highly productive seaweeds like the sea lettuce, Ulva, can take advantage of these nitrogen spikes by rapidly storing nitrogen for later use. Other more massive and slower growing seaweeds like Codium do not have this ability (Ramus and Venable 1987), but may gain additional nitrogen by establishing symbiotic associations with nitrogen fixing blue-green algae (Rosenberg and Paerl 1980).

2.4 CURRENTS

The most important offshore current in the region is the Florida Current, which originates in the Florida Straits between Florida and Cuba. It is joined by the north flowing Antilles Current, which runs along the outer edge of the Continental Shelf. The Florida Current moves offshore at Cape Hatteras to become the Gulf Stream, although this latter name is often applied to the Florida Current as well. The position of the Florida Current varies seasonally. In the summer it moves inshore, bringing warm, clear water to the shelf. In the winter it is driven offshore by northerly winds. When this happens cold water from the north may move

south along the North Carolina coast past Cape Hatteras (Gray and Cerame-Vivas 1963; Stefansson et al. 1971). Inshore currents south of Cape Hatteras are variable. South-flowing geostrophic currents are periodically interrupted by inshore movement of the Florida Current, which forces a northward flow (Bumpus 1973). However, the general direction of longshore drift is from north to south.

2.5 TIDES AND WAVES

The mean tidal range is less than 1.5 m along the coast of North Carolina, increases in South Carolina, and reaches a maximum of 2 m in Georgia (Figure 4).

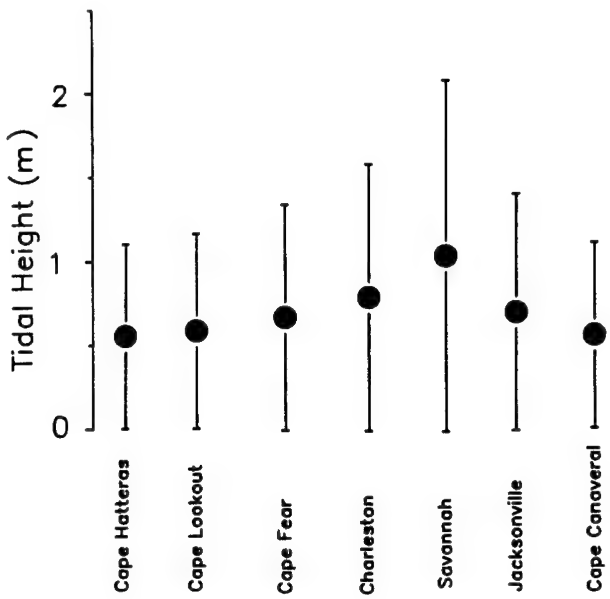


Figure 4. Mean tide level and mean tidal range in the South Atlantic Bight (U.S. Department of Commerce 1987).

South of Georgia the tidal range decreases again, and is only 1 m at Cape Canaveral, FL. In the classification of Davies (1964), the South Atlantic Bight is micro-tidal (tidal range <2 m) along the North Carolina coast, meso-tidal (tidal range >2 and <4 m) in southern South Carolina and Georgia and micro-tidal once again in central Florida.

Wave height varies inversely with tidal range (Nummedal et al. 1977). Mean annual wave heights range from 1.7 m at Cape Lookout, NC, to 0.8 m at Jacksonville, FL. The inverse relation of tidal range and wave height produces barrier islands and tidal inlets of different types. This is discussed in Chapter 5.

2.6 SEDIMENTS

Most sand found on the beaches in the South Atlantic Bight comes from the adjacent Continental Shelf (Neal et al. 1984). It is pushed up to the beach by fair-weather waves. Sand is carried laterally by longshore currents that move in the surf zone parallel to the beach. In general, this movement is from north to south in the South Atlantic Bight, although this can be reversed by a variety of local factors. Massive relocation of sediments can occur during hurricanes and winter storms, called northeasters. This relocation depends on the interaction of longshore currents, tides, and waves and is discussed in Chapter 5. In the Southeastern United States, most sediment carried to the coast by rivers is deposited near the heads of estuaries (Neal et al. 1984). However, some of this sediment is eventually resuspended by wave and tidal action and is moved out through inlets into the longshore sediment transport system.

CHAPTER 3. COMMUNITY DESCRIPTION

Rubble-structure communities consist of, and interact with, a wide variety of different flora and fauna including: plankton, seaweeds, invertebrates, fishes, and birds. This chapter describes the most apparent groups of organisms associated with rubble structures and, where appropriate, discusses prominent species and their patterns of recruitment and distribution. Feeding habits and basic natural history are also treated here. Detailed aspects of the ecology of these organisms and communities are discussed at length in the following chapter on ecological patterns and processes.

3.1 PLANKTON

Both phytoplankton and zooplankton serve as important foods for benthic filter feeders and for some juvenile fishes on jetties. The availability of these foods may change on time scales of hours, days, or seasons (Harris 1980; Litaker et al. 1987). This is especially true on inlet jetties, which are affected by oceanic waters at high tide and by more productive, estuarine waters at low tide. There are also significant seasonal and diel effects caused by interactions among rainfall, evaporation, terrestrial runoff, and diel patterns in phytoplankton growth (Litaker et al. 1987). As an example, in winter the estuarine waters behind the Outer Banks of North Carolina are dominated by riverine inputs because of high rainfall and low evaporation. Growth-limiting nitrogen is supplied as nitrate and ammonium by runoff from the drainage basin. In summer, the lower rainfall and higher evaporation rates cause this area to function more like a lagoon. Most nitrogen is supplied as ammonium due to biological regeneration. In winter, diel changes in phytoplankton abundance are small. In summer, an outgoing tide in late afternoon can have twice the abundance of phytoplankton as an outgoing tide in early morning (Litaker et al. 1987).

Zooplankton communities are composed of permanent zooplankters (holoplankton), such as copepods, and of the larvae of benthic organisms (meroplankton), including those on rubble structures. There are large fluctuations in density and species composition of holoplanktonic organisms. These are due to seasonal and diel changes in temperature, and predation by fish and other zooplankters (Fulton 1983, 1985). Fluctuations in the abundance of larvae from the benthos could be affected by the same factors but will also be significantly affected by the timing of larval release.

3.2 SEAWEEDS

Community Composition

Most of the South Atlantic Bight is an inhospitable habitat for seaweeds because of the large expanses of unconsolidated sands, silts, and muds to which most seaweeds cannot attach. Natural intertidal rocks are rare, occurring at only a few places near the border between North and South Carolina, and at Marineland, FL. On the Continental Shelf, there are outcrops of sedimentary rocks that start just south of Cape Hatteras and run all the way to Florida. However, most of these outcrops are covered by sediment and so are not available for attachment by seaweeds. Hard substrates that are available for attachment occur most abundantly in Onslow Bay, NC, and on the coast near Palm Beach,

FL (Searles 1984). Because natural hard substrates are rare in the bight, most seaweeds are attached to shell fragments, other algae, seagrasses, or to introduced substrates such as seawalls, jetties, and docks.

Between Long Island Sound and Cape Hatteras, there are approximately 150 species of red (Rhodophyta), brown (Phaeophyta), and green (Chlorophyta) seaweeds (Searles 1984). Between Cape Hatteras and Cape Canaveral, there are approximately 320 species; 303 of these are known from North Carolina (Searles 1984). Ninety-five species occur in South Carolina (Wiseman and Schneider 1976; Wiseman 1978; Blair and Hall 1981), 81 species occur in Georgia (Chapman 1971, 1973; Searles 1981, 1984), and only 43 are reported in Florida north of Cape Canaveral (Humm 1952). However, Humm (1952) probably underestimates the number of species in the area since 234 species occur between Cape Canaveral and Palm Beach (Kerr 1976; Eiseman 1976, 1979; Eiseman and Moe 1981; Eiseman and Norris 1981; Hall and Eiseman 1981). There are several reasons why North Carolina appears to have 3 to 4 times the number of seaweed species as South Carolina or Georgia. These include (1) the location of North Carolina in a transitional zone between the temperate seaweeds of New England and the tropical seaweeds of the Caribbean, (2) the greater abundance of hard substrates off the North Carolina coast, and (3) the greater number of seaweed specialists that have investigated the marine flora of North Carolina. Because of the extensive floristic investigations conducted in North Carolina by Searles, Schneider, and Kapraun (Schneider 1976; Searles and Schneider 1978, 1980; Schneider and Searles 1979; Kapraun 1980a, b, 1984; Kapraun and Zechman 1982; Searles 1984), the seaweeds of this area are much better known than those in any other part of the South Atlantic Bight. The paucity of data from other regions forces us to focus most of our discussion on the seaweeds of the Carolinas. For keys and illustrations of seaweeds of the South Atlantic Bight, see Taylor (1960) and Kapraun (1980a, 1984).

The seaweeds growing highest in the intertidal zone are usually blue-green algae that appear as a darkly colored band on the rocks (Figure 5). The most common seaweeds immediately below the blue-green zone are usually the green algae, Ulva, Enteromorpha, and Cladophora, and, at times, the red alga Porphyra. Ulva and Enteromorpha (Figure 6) are bright green seaweeds that often grow intermixed. They are distinguished primarily on the basis of frond morphology. Ulva has a flat membranous frond composed of two cell layers; Enteromorpha fronds are similar except that they are tubular, at least in part. Since some species of Enteromorpha

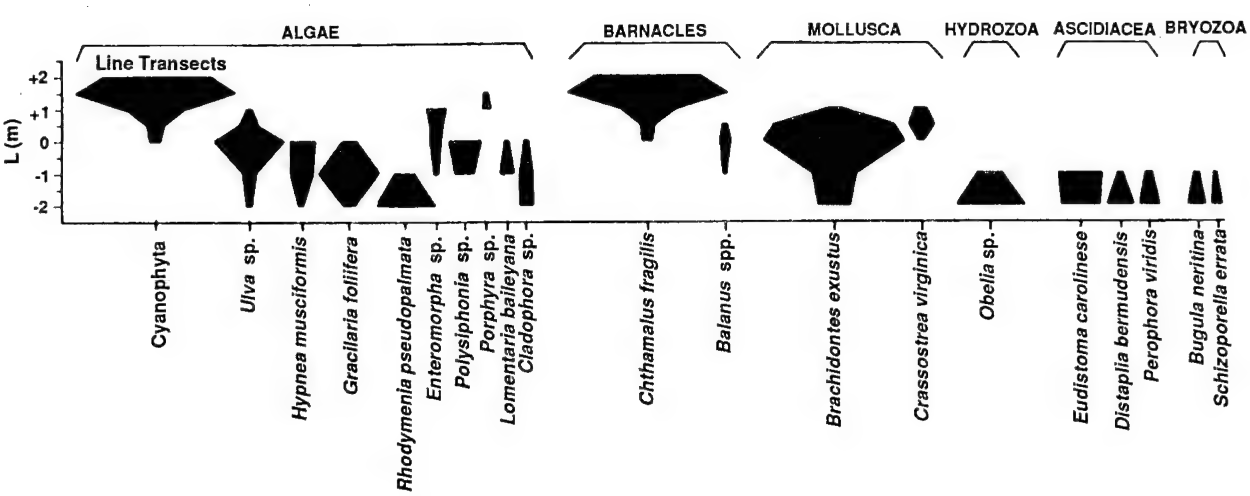


Figure 5. Vertical distribution (L=level with respect to Mean Tide Level) of the 20 most abundant sessile species observed at north jetty stations at Murrells Inlet, SC. Band width indicates abundance (Van Dolah et al. 1984).

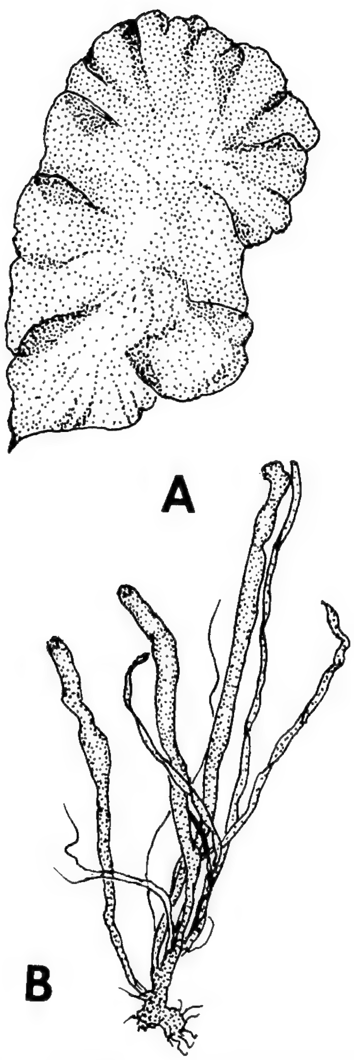


Figure 6. The common green seaweeds (A) *Ulva*, and (B) *Enteromorpha*.

have broad flat blades with tubular morphology only along the margins (i.e. superficially like *Ulva*), some members of this genus are difficult or impossible to distinguish from *Ulva* without a microscope. In culture, some *Ulva* species produce tubular progeny, suggesting that distinctions between the two genera are questionable. *Cladophora* is one of the most common genera of small green filamentous algae. It can easily be confused with a number of other algae by nonspecialists. The red alga *Porphyra* is *Ulva*-like in morphology but is usually brown to purple in color.

The lower intertidal zone is usually occupied by a mixed species group of red seaweeds (Figure 5). Several small filamentous forms such as *Polysiphonia*, *Herposiphonia*, *Audouinella*, and *Erythrotrichia* are common, but these are difficult to identify without magnification. *Hypnea musciformis* is a very common larger seaweed with bushy, cylindrical branches that often end in fish-hook like tendrils that are used to attach secondarily to other seaweeds (Figure 7). Like many of the red (Rhodophyta) seaweeds, it may be deep green, red, straw-colored, or some

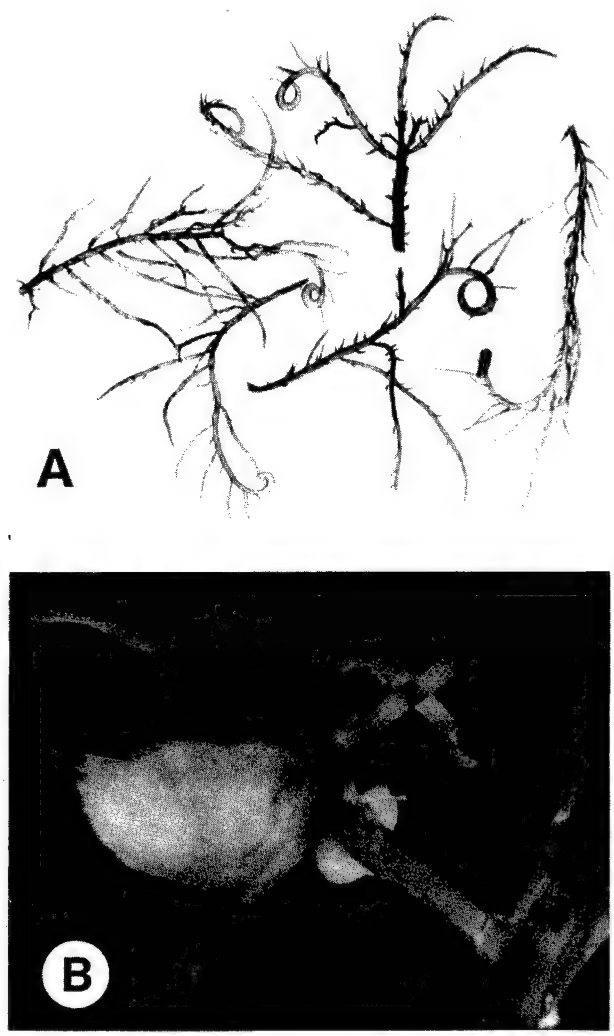


Figure 7. (A) The common red seaweed *Hypnea musciformis*. Its hook-shaped branch tips often facilitate its attachment to other seaweeds. (B) shows a close-up of a *Hypnea* tip that has attached around the base of a *Sargassum* float.

combination of the three. Lomentaria is a rose to red-colored plant that looks like Hypnea but does not have recurved tips. It forms densely branched creeping mats, has hollow axes except at the bases, and its branchlets tend to arch back toward the main axis. Gracilaria tikvahiae (formerly G. foliifera) is olive green to dark red and has flattened, strap-like blades with pointed tips (Figure 8A). Although the entire plant may appear irregularly bushy, the branches along each main axis all branch in the plane of the blade. Rhodymenia pseudopalmata is rose to red in color and has strap shaped, dichotomously branching blades with rounded tips. It usually occurs at, or below, the low tide line. Small, wiry turfs of reddish-purple to brown seaweeds in the genus Gelidium also occur in this same habitat.

On some jetties, green, sponge-like, dichotomously branching algae (Figure 8B) in the genus Codium (commonly called dead man's fingers) are common at this low tidal level. In North Carolina, jetties have traditionally supported populations of Codium decorticatum and Codium isthmocladium. Within the past decade, the introduced species Codium fragile has invaded down the coast from New England and now makes up a substantial portion of the Codium biomass on local jetties (Searles et al. 1984; J. Ramus, Duke University Marine Laboratory, Beaufort, NC; pers. comm.).

Virtually all of the genera and species mentioned above also occur in the shallow subtidal zone during some times of the year or in some locations. The distinction between intertidal and subtidal seaweeds in the South Atlantic Bight is not always clear and appears to be useful only during some times of the year (Kapraun and Zechman 1982). However, several jetty seaweeds are almost exclusively subtidal.

The most abundant subtidal seaweed on jetties along much of the coast is the brown alga Sargassum. It has a wiry main axis, linear leaves with midribs, and stalked, spherical air bladders (Figure 8C). In summer, the brown seaweeds Padina and Dictyota are also common. Padina forms a fanshaped, lightly calcified blade (Figure 8D); Dictyota has membranous, dichotomously branched axes that are brown to golden brown in color (Figure 8E).

Several other seaweeds are occasionally common in the subtidal zone including: the green alga Bryopsis; the red algae Chondria (Figure 8F), Callithamnion, Champia, Dasya, Hypoglossum, Calonitophyllum, and Grinnellia; and the brown algae Ectocarpus, Punctaria, and Petalonia. Given the difficulties associated with seaweed identification, readers interested in seaweeds should consult Taylor (1960) or Kapraun (1980a, 1984) before assigning a name to any seaweed from this coast.

Distribution

When researchers study algal communities on rubble structures in the South Atlantic Bight at a single point in time (usually summer), they often describe distinct patterns of zonation based primarily on the upper limits of dominant species (Hoyt 1920; Williams 1949; Earle and Humm 1964). When Kapraun and Zechman (1982) investigated seasonal patterns of vertical zonation on jetties at Masonboro Inlet, NC, they noted what appeared to be relatively distinct intertidal and subtidal communities in the summer, but during the remainder of the year there was no clear separation of communities at the low tide line. During winter and early spring, so called intertidal species like Porphyra carolinensis and Enteromorpha prolifera became abundant in the subtidal zone, but during the summers, they retreated back to the intertidal. Kapraun and Zechman (1982) hypothesized that these changes occurred in response to changing competitive interactions among the plants. However, these changes are also consistent with the hypothesis that fish grazing during the warm portions of the year, when fishes are most numerous, exclude these palatable seaweeds from the subtidal zone. The limited available data suggest that fishes drive several palatable seaweeds to near extinction on subtidal portions of jetties in the summer (Hay 1986). Additionally, recent work in outdoor microcosms has shown that Enteromorpha grows year round in the subtidal zone if fishes are excluded from the system (Hay 1986). If fishes are abundant,

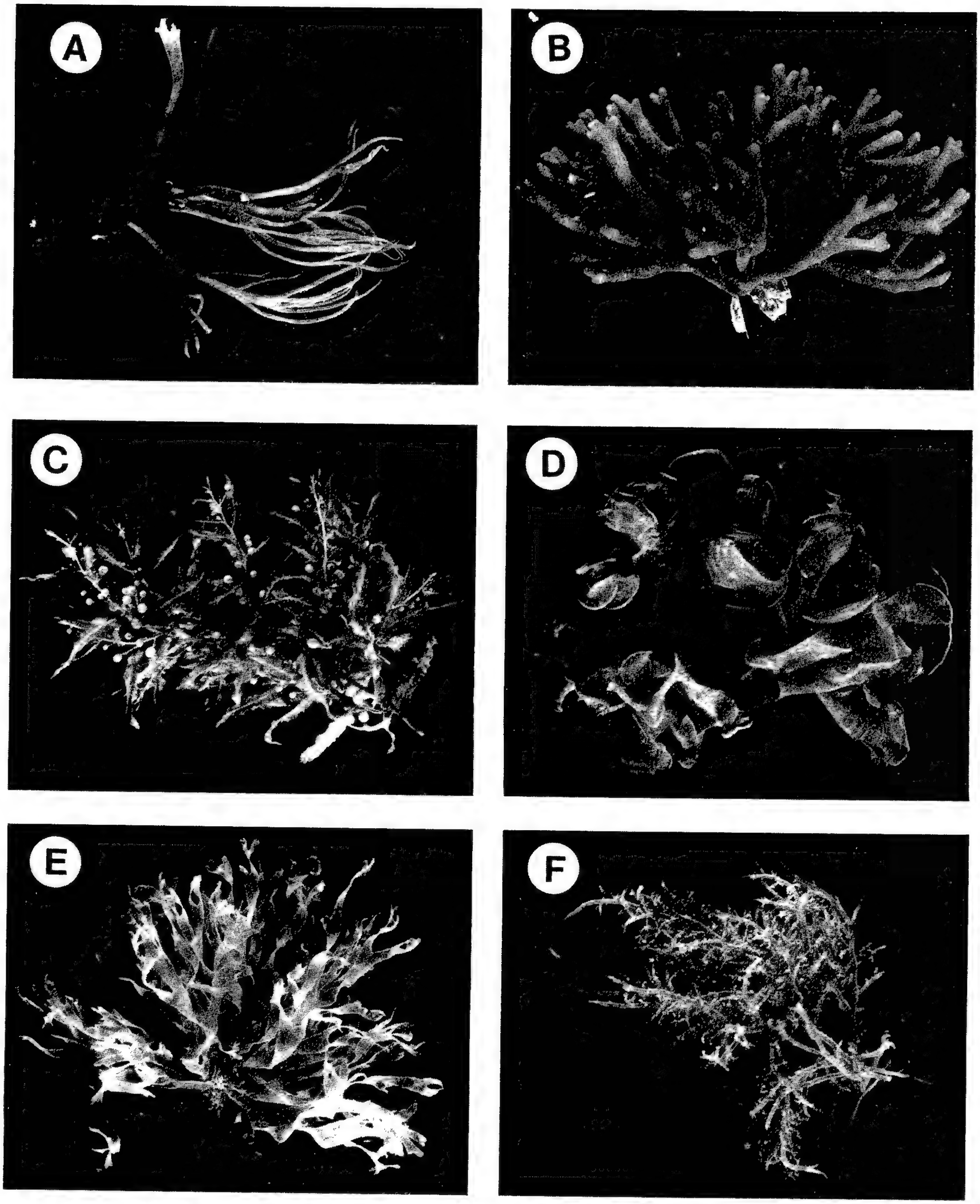


Figure 8. Some common seaweeds on jetties in the South Atlantic Bight. (A) *Gracilaria tikvahiae*, (B) *Codium* sp., (C) *Sargassum filipendula*, (D) *Padina gymnospora*, (E) *Dictyota dichotoma*, and (F) *Chondria* sp.

Enteromorpha is driven locally extinct in the subtidal zone or occurs only in small refuge areas.

The most extensive studies of the spatial distributions of seaweeds in the bight focus on the distinctions between nearshore and offshore species and on how they are distributed north-to-south along the U. S. coastline (Schneider 1975, 1976; Searles and Schneider 1980; Searles 1984). Of the 303 seaweeds known from North Carolina, approximately two-thirds occur in shallow coastal habitats and are potential residents of rubble structures. Approximately one-half (109 species) of the 204 species found in shallow water are not known to occur in deep offshore waters. Of the 194 species that do occur in deep offshore waters, approximately one-half (108) are known only from those depths. About one-third (96 species) of the total flora have been collected in both shallow and deep habitats.

For the shallow water species, 21 reach their northern limit and 27 reach their southern limit of distribution in North Carolina. Within North Carolina, the Cape Lookout jetty appears to be the northernmost limit in the intertidal zone for tropical and subtropical seaweeds (Williams 1948; Humm 1969; Schneider 1976). The Continental Shelf off Cape Lookout plays a similar role for the offshore seaweeds (Schneider 1976). A few reach the southern limit of their distribution off Cape Lookout (only 1%), but many (37%) reach their northern-most limit there. This indicates the more tropical affinity of the offshore flora. Of the 303 seaweeds known from North Carolina, 44% reach their northern limits and 10% reach their southern limits within the State.

In the Carolinas, seasonal changes in the occurrence, abundance, and reproduction of algal species can be dramatic (Schneider 1975, 1976; Richardson 1979, 1981, 1982; Kapraun and Zechman 1982; Peckol 1982; Peckol and Searles 1983; Van Dolah et al. 1984). In a study of seaweeds on an intertidal jetty, Kapraun and Zechman (1982) noted that the red algae were most diverse in summer, brown algae were most diverse in winter, and green algae were relatively aseasonal. They also suggested that there were three components of the North Carolina algal community they studied: 1) a eurythermal cool-temperate element in winter (comprising 37% of the species at their site); 2) a eurythermal tropical element in summer (comprising 18% of the species at their site); and 3) a larger, warm-temperate element that occurred year round (comprising 45% of the species at their site). Schneider (1975, 1976) studied the flora of the Continental Shelf and noted maximal development in mid-summer. The number of species and total biomass decreased in fall, reached a yearly low in winter, and then increased spring through summer. Ninety-nine percent of all species were present in mid-summer, 59% were present in the fall, and only 33% were present in the winter.

Successional patterns have not been adequately documented for shallow water seaweeds in the bight. Van Dolah et al. (1984) documented the summertime abundance of seaweeds on jetties at Murrells Inlet, SC, every year for 4 years after construction. Between the first and second year there was an increase in the number of algal species and in algal abundance. Changes between the second and fourth years were nondirectional.

Patterns of Recruitment

Seaweeds may recruit via various types of spores or, in some species, by fragmentation and reattachment of adult portions (Dixon 1965). Given the seasonally changing nature of the flora of the South Atlantic Bight, reinvasion following seasons of inhospitable conditions could be a major problem for benthic seaweeds. Many seaweeds appear to have adapted to these conditions by persisting throughout unfavorable periods as stunted forms or persistent holdfasts; Sargassum filipendula, Botryocladia occidentalis, and Gracilaria mammillaris do this in Continental Shelf habitats (Schneider 1976). Several species on shallow jetties in the bight produce early developmental stages that are capable of withstanding long periods of unfavorable conditions. This phenomenon has been studied in greatest detail by Richardson (1978, 1979, 1981, 1982).

On the jetty at Radio Island, NC, the brown seaweeds Dictyota dichotoma, Padina gymnospora (formerly P. vickersiae), and Dictyopteris membranacea overwinter as early developmental stages (Richardson 1978). Of these three species, Dictyota has been studied in greatest detail (Richardson 1979). Dictyota is visibly present from mid-April to December and releases propagules continuously during this growing season; in most instances, these spores rapidly germinate and grow into mature plants. Neither spore release nor attachment are affected by temperature or photoperiod. However, germination and establishment are temperature dependent. Spores cannot germinate in winter. However, if there is an initial warm period of 5-6 days, the spores germinate and the resulting sporlings can survive several months of winter conditions. Thus, microscopic sporlings produced at the end of the growing season, overwinter and assure the continuation of the population when warmer conditions return.

The red alga Dasya baillouviana is apparent on the jetty between February and May (i.e., the opposite of the pattern shown by Dictyota). In April or May it reproduces and disappears. Like Dictyota, it persists as a young developmental stage during those times of year when it is not evident (Richardson 1981). Each winter, a single generation of plants grows, reproduces, and releases spores that settle but do not develop into visible plants until the following growing season. In Cape Cod, D. baillouviana persists through winter as a sporeling but produces multiple generations during its growing season (Sears 1971). In the tropics, D. baillouviana grows year round as a visible plant (Mathieson and Dawes 1975).

The green alga Bryopsis plumosa exhibits a pattern somewhat similar to Dasya and Dictyota. It is visibly present from January until May, and persists through the summer and fall as a prostrate microthallus stage (Richardson 1982).

Amsler and Searles (1980) investigated the distribution of algal spores in a 20 m water column 30 km off the coast of North Carolina. Spores of green algae were distributed throughout the column and spores of bangiophycean red algae (the simpler red algae like Porphyra) were present at all depths but concentrated in greatest abundance near the bottom. Spores of brown and florideophycean red algae (the more complex red algae like Hypnea and Chondria) occurred almost exclusively near the bottom. Green and bangiophycean red algae tended to be more opportunistic than brown and florideophycean red algae, suggesting that this distribution of spores is adaptive in that it allows for wide dispersal of the opportunistic species (carried with the surface curents) and keeps the less opportunistic species near habitats where the parents were successful.

Epiphytic Algae

Several species of algae can use other seaweeds as substrates for attachment (Figure 7). A host of small algae (diatoms, filamentous blue-green, red, brown, and green algae) and several larger macrophytes (such as Hypnea, Spyridia, Enteromorpha, Chaetomorpha, and Dictyota) commonly occur as epiphytes. Growing epiphytically can provide a mechanism for circumventing competitive exclusion when all primary substrate is occupied (Hay 1981a; Hawkins and Harkin 1985). Epiphytes may also avoid herbivorous fishes, which visit large unpalatable plants less often than they do smaller, more palatable ones (Hay 1986). Some specialized epiphytes may obtain nutrients from the host (Harlin 1973; Goff 1976).

In situations where consumption by fishes does not severely reduce their numbers, small crustaceans that graze epiphytes can occur at densities of several thousand/m^2 in stands of macroalgae. In some cases, grazing by these small crustaceans can keep larger seaweeds relatively free of fouling epiphytes (Brawley and Adey 1981a, b). These highly productive epiphytes are very important in maintaining the high density and turnover rate of small crustaceans that are such an important component of the diet of fishes on rubble structures (see later sections).

3.3 INVERTEBRATES

Community Composition

In the intertidal zone, sessile invertebrates consist largely of barnacles, oysters, and mussels (Figure 9) (Stephenson and Stephenson 1952, 1972; Wood 1968; Ortega 1981; Van Dolah et al. 1984; Fox and Ruppert 1985). The smallest barnacle is Chthamalus fragilis (Figure 9A), which is white, easily destroyed with a fingernail, and has no calcareous basal plate. Other barnacles in the genus Balanus are larger, more robust, and have calcareous basal plates. B. improvisus is white, with a diamond or kite-shaped aperture (Figure 9B). B. trigonus has a similar shaped aperture, but the shell plates are rough, with red and white coloration. B. eburneus is white, but has a pentagonal-shaped aperture (Figure 9C). B. amphitrite has purple stripes on the shell plates. In the south, the much larger, solid-walled barnacle, Tetraclita squamosa v. stalactifera, becomes common. Bivalves are represented by the common oyster Crassostrea virginica, and the small black mussel Brachidontes exustus, which forms mats (Figure 9D, E).

There are a few mobile organisms that are intertidal, including the large isopod Lygia exotica, the predatory Atlantic oyster drill, Urosalpinx cinerea (Figure 10E), and in the south, the siphonarid limpet Siphonaria pectinata. Where the structural matrix of the oyster zone is well developed, it provides a habitat for xanthid crabs such as Panopeus herbstii (Figure 10B).

Mussels and oysters are generally absent subtidally, and the sessile animal community consists of sponges, coelenterates (anemones and hydroids), bryozoans, tunicates, and barnacles (McDougall 1943; Maturo 1959; Wells et al. 1960, 1964; Sutherland 1974, 1977, 1978, 1981; Sutherland and Karlson 1977; Karlson 1978; Mook 1981, 1983a, b; Van Dolah et al. 1984; Fox and Ruppert 1985). Except for the absence of Chthamalus fragilis, the barnacles are the same as those found in the intertidal zone.

One of the most common sponges is Microciona prolifera, which is bright red

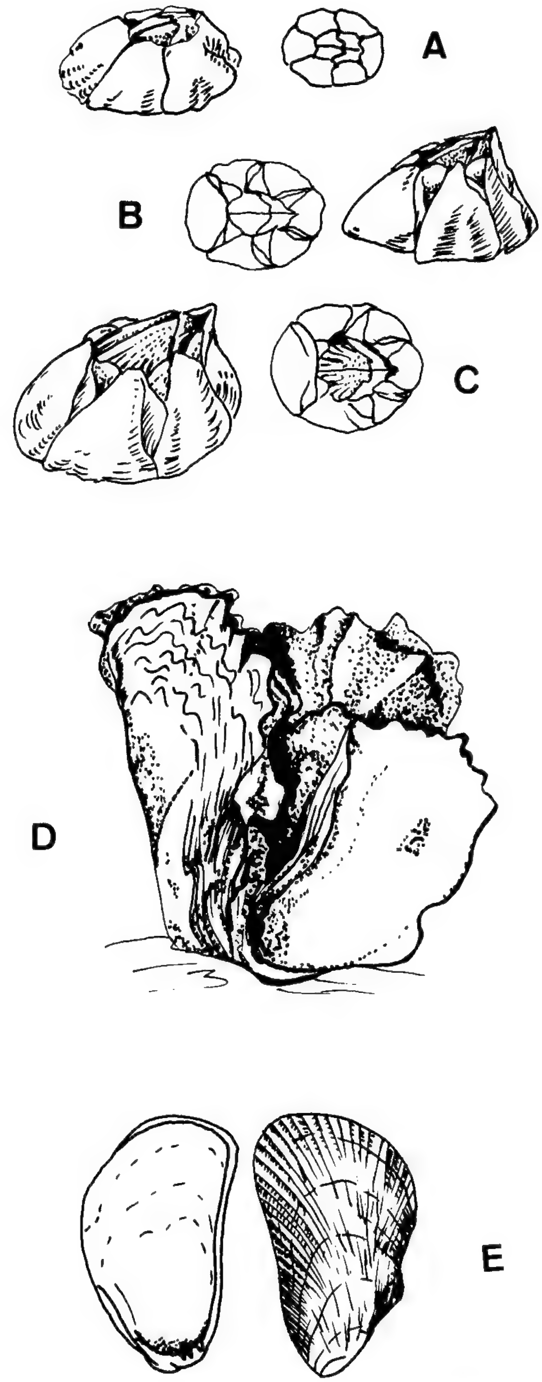


Figure 9. Common intertidal invertebrates. (A) *Chthamalus fragilis* (to 8 mm diameter), (B) *Balanus improvisus* (to 13 mm diameter), (C) *Balanus eburneus* (to 25 mm diameter), (D) *Crassostrea virginica* (to 150 mm length), and (E) *Brachidontes exustus* (to 35 mm length). A, B, and C redrawn from Lippson and Lippson (1984), D and E redrawn from Van Dover and Kirby-Smith (1979).

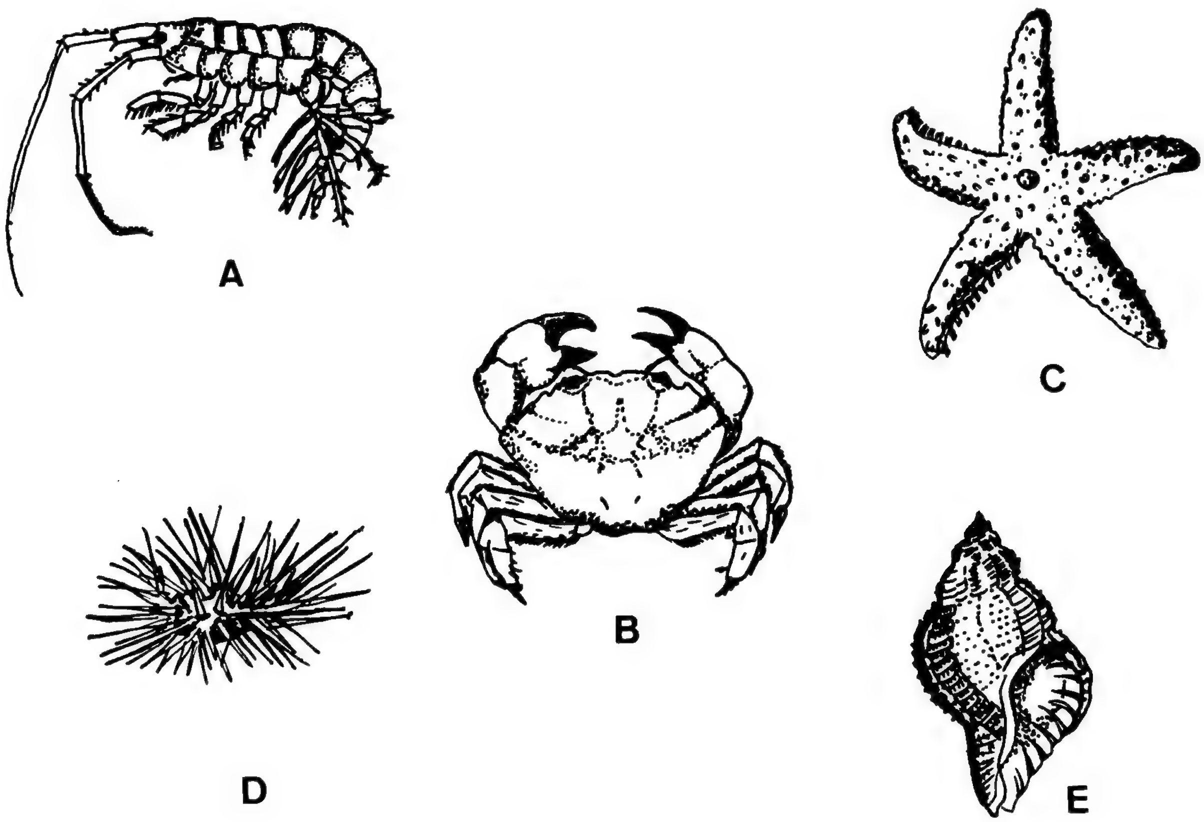
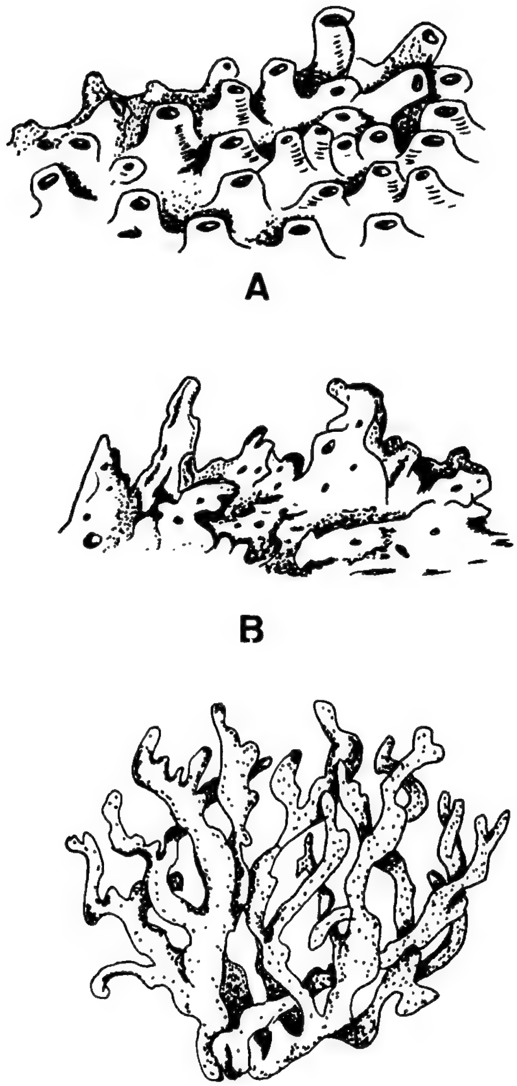


Figure 10. Common mobile invertebrates. (A) *Ampithoe longimana* (to 10 mm length), (B) *Panopeus herbstii* (to 25 mm length), (C) *Asterias forbesii* (to 150 mm diameter), (D) *Arbacia punctulata* (to 50 mm diameter), and (E) *Urosalpinx cinerea* (to 25 mm height). All redrawn from Van Dover and Kirby-Smith (1979).

and can be encrusting or erect with finger-like projections (Figure 11C). Next in intensity of color is the bright orange, massively encrusting Xestospongia halichondrioides. Other sponges are rather drab. Mycale cecila is thinly encrusting, slimy, and a pale yellowish green or yellowish tan. Halichondria bowerbanki assumes a variety of shapes, starting as low encrustations, but often developing a mass of ridges or branches (Figure 11B). It is straw yellow, beige, or pale orange in color. A number of species of Haliclona (Figure 11A) may be found which are difficult to tell apart without reference to spicules. They are generally encrusting, softly spongy, and gray, tan, or pinkish brown in color. Finally, Lissodendoryx isodictyalis is a thickly encrusting sponge with a crisp consistency and is blue-green or yellow-green in color. When broken open it is said to smell of garlic. Because of the variation in color and shape, spicules should be examined for positive identification (Wells et al. 1960).

Tubularia crocea is one of the most conspicuous hydroids, forming large tufts of long, unbranched stalks topped with pink zooids (Figure 12B). Other common hydroids are the white, delicate Obelia dichotoma, Eudendrium carneum with its intensely orange colonies, and Halocordyle disticha (=Pennaria tiarella), which has a long black central stalk with two pinnate rows of side branches bearing polyps (Figure 12A). In protected waters Hydractinia echinata forms a white, fuzzy encrustation over the substrate. Other



A

B

C

Figure 11. Common sponges (A) *Haliclona* sp. (colony to 8 cm wide), (B) *Halichondria bowerbanki* (colony to 8 cm high, 30 cm wide), and (C) *Microciona prolifera* (colony to 20 cm high, 30 cm wide). All redrawn from Lippson and Lippson (1984).

common coelenterates are the large sea whip Leptogorgia virgulata (Figure 12C), the small stony coral Astrangia danae, and the larger, branching coral Oculina arbuscula. Anemones include Bunodosoma cavernata which is large and warty, Aiptasia pallida (Figure 12D), which is small and pale brown, and Diadumene leucolena, which is pale and translucent.

The most abundant foliose bryozoan is Bugula neritina, with its red-purple bushy colonies (Figure 13B). B. stolonifera is similar in morphology to B. neritina, but white in color. Anguinella palmata is another foliose bryozoan but it has gray, nondescript colonies. Alcyonidium hauffi is a gray-brown, rubbery bryozoan often found encrusting the stalks of other bryozoans and hydroids. There are two common encrusting bryozoans that can be distinguished largely on the basis of color; white colonies are probably Membranipora tenuis and orange colonies are probably Schizoporella errata (Figure 13A).

Colonial tunicates are also conspicuous features of the sessile fauna. Eudistoma carolinense forms thick, irregular sandy encrustations, while its congener Eudistoma hepaticum is purple and liver-like. Didemnum candidum forms thin, pure white encrustations. Clavelina oblonga is a semicolonial tunicate with elongate, clear, colorless zooids that are joined together only at the base. Distaplia bermudensis comes in many colors--red, orange, and purple--and has relatively large zooids embedded in the common tunic. The individual intake apertures are arranged in circles around a common exhalent opening. Aplidium constellatum is red-orange to white, hemispherical and looks like a small brain attached to the rocks. Its congener A. stellatum forms whitish, tough, plate-like colonies with orange-red zooids arranged in a stellate pattern (Figure 14C). Both are called "sea pork" by local fishermen. Perophora viridis looks like small, green grapes connected with green stolons and is often found in the canopy of other hydroids and bryozoans. Diplosoma macdonaldi forms thin, transparent sheets which contain the black zooids. Also seen are the gold-purple-brown, loose blob-like rolls and lobes of Botryllus schlosseri, especially in North Carolina. In South Carolina and northern Florida more tropical forms are found, such as the pinkish, gelatinous, encrusting Symplegma viride, with its brightly colored zooids. Solitary tunicates are represented by the gray globes of Molgula manhattensis (Figure 14B), the tough, wrinkled, tan individuals of Styela plicata (Figure

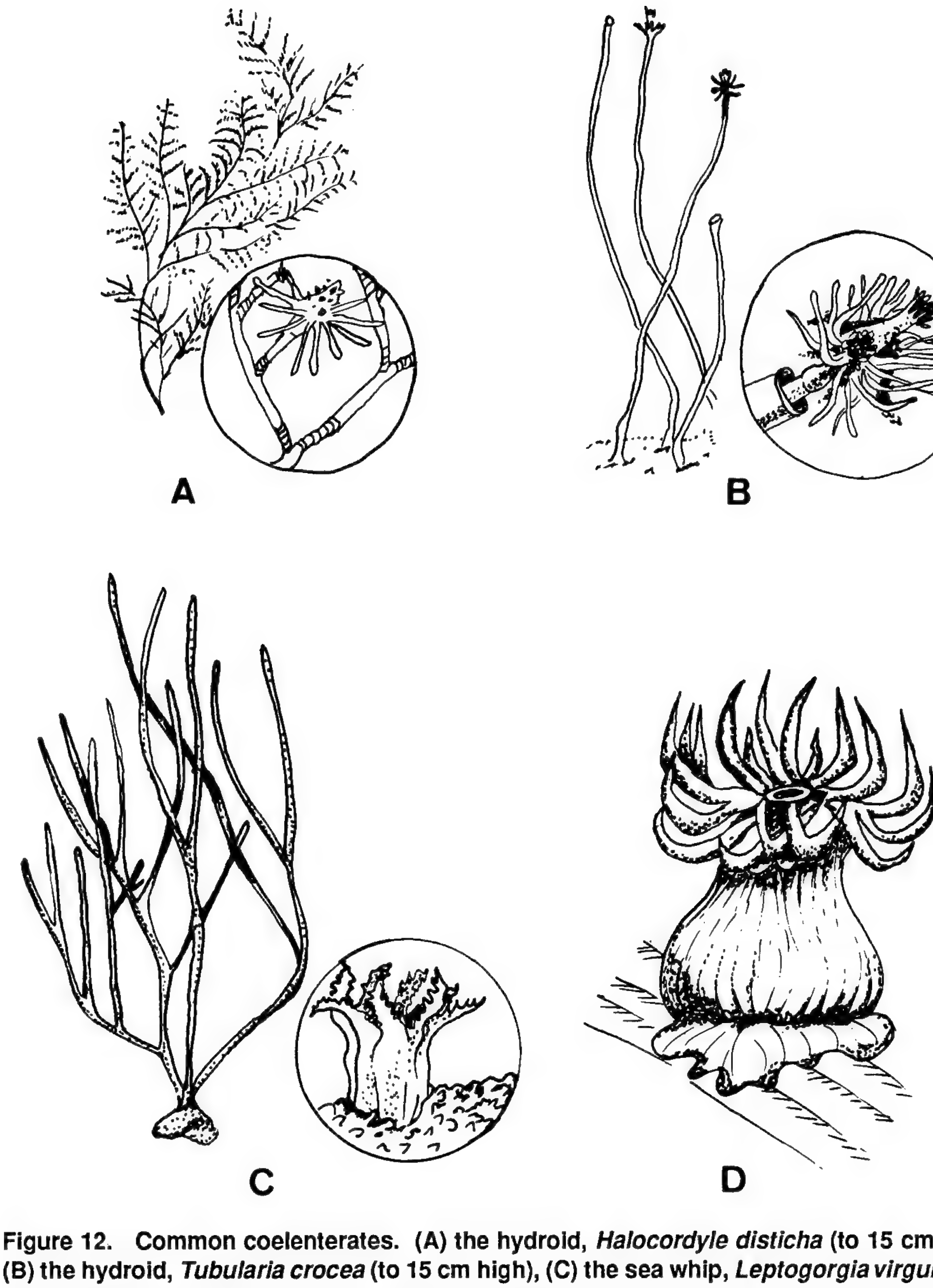


Figure 12. Common coelenterates. (A) the hydroid, *Halocordyle disticha* (to 15 cm high), (B) the hydroid, *Tubularia crocea* (to 15 cm high), (C) the sea whip, *Leptogorgia virgulata* (to 60 cm high), and (D) the anemone, *Aiptasia pallida* (to 3 cm high). A, B, and C redrawn from Lippson and Lippson (1984), D redrawn from Spitsbergen (1980).

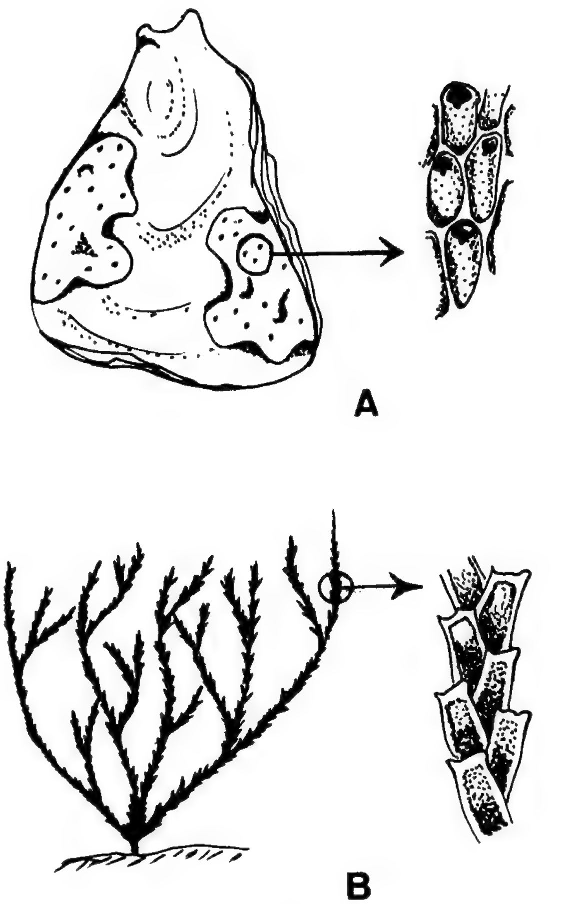


Figure 13. Common bryozoans. (A) *Schizoporella errata* (colony to 30 cm wide), and (B) *Bugula neritina* (to 12 cm high). Redrawn from Spitsbergen (1980).

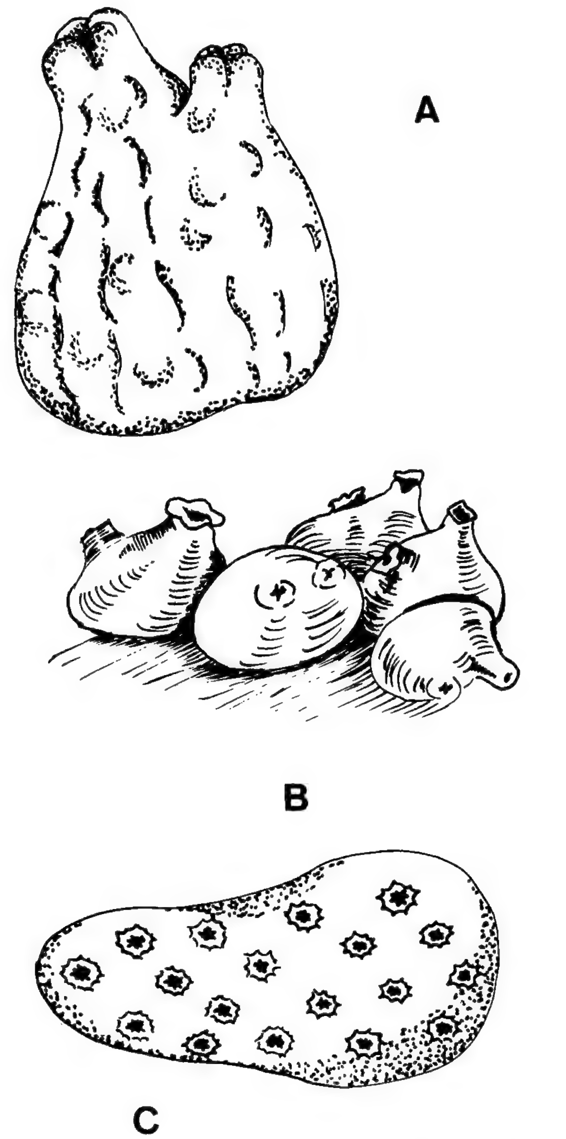


Figure 14. Common tunicates. (A) *Styela plicata* (to 13 cm high), (B) *Molgula manhattensis* (to 4 cm high), and (C) *Aplidium stellatum* (colony to >30 cm wide). B redrawn from Lippson and Lippson (1984), C redrawn from Gosner (1978).

14A), and the pale green Ascidia interrupta.

Large motile subtidal invertebrates include the starfish Asterias forbesii (Figure 10C), the purple sea urchin, Arbacia punctulata (Figure 10D), the stone crab, Menippe mercenaria, and the blue crab, Callinectes sapidus. The most common crab is the somewhat smaller, orangish mud crab Neopanope sayi. Hermit crabs are represented by the flat-clawed Pagurus pollicaris, the long-clawed Pagurus longicarpus, and the much larger Clibanarius vittatus, which has yellow stripes on the walking legs. The small, tube-building gammarid amphipods Ampithoe (Figure 10A) and Corophium spp. are common in summer. In winter, caprellid amphipods (Caprella spp.) are abundant. Many kinds of snails are present, including the small, seed-shaped, brown lunar dove snail, Astyris lunata, the larger greedy dove snail, Anachis avara, the sculptured top snail, Calliostoma euglyptum, the Atlantic oyster drill, Urosalpinx cinerea and the Florida rock shell, Thais hemastoma floridana.

Distribution

On exposed jetties the supralittoral fringe is blackened by blue-green algae, over which wanders the occasional isopod Lygia exotica (Figure 5; Van Dolah et al. 1984; Fox and Ruppert 1985). Below this is a barnacle zone, usually with Chthamalus fragilis occupying the highest levels and various species of Balanus at lower levels (Figure 5). Barnacles can be abundant, approaching 100% cover (Ortega 1981). Below the barnacle zone at mid-intertidal levels, is a zone where the oyster Crassostrea virginica reaches its highest abundance, although this rarely exceeds 20% cover in exposed habitats (Figure 5; Ortega 1981). Below the barnacle and oyster zones is a zone with high densities of the mussel Brachidontes exustus, which reaches to mean low water (Figure 5). This pattern of zonation is found with minor modifications throughout the South Atlantic Bight, although in northern Florida we begin to see a more tropical fauna. Balanus spp. give way to the larger barnacle Tetraclita squamosa and the siphonarid limpet Siphonaria pectinata becomes abundant in the mid-intertidal zone (Stephenson and Stephenson 1972).

A similar pattern of zonation is seen on more protected rubble structures except that the lower intertidal zone is dominated by the oyster Crassostrea virginica instead of the mussel Brachidontes exustus (Ortega 1981).

Subtidally, our information is biased towards shaded habitats in protected waters of North Carolina, where most work has been conducted. The hallmark of the shallow subtidal community is change. In their studies at Beaufort, NC, Sutherland and Karlson (Sutherland and Karlson 1977; Karlson 1978; Sutherland 1981) found that the longevity of most community members was less than a year. Few species appeared able to tolerate the entire 25 ^{o}C annual temperature range at Beaufort. Hydroids and tunicates were especially seasonal. Short life spans also contributed greatly to seasonal changes in species composition.

Characteristically, mature benthic assemblages were invaded by the tunicate Styela plicata each spring. Small individuals often grew epizootically (on top of other invertebrates) and after a summer of rapid growth became too heavy for their attachment sites. S. plicata commonly sloughed off in the fall, taking many other adhering organisms with it. This process produced bare spaces on the substrate, which were most often filled with newly recruiting larvae. Variations in larval recruitment produced winter assemblages dominated by a variety of sponges, hydroids, and bryozoans. Summer assemblages were dominated by the solitary tunicate S. plicata and the foliose bryozoan Bugula neritina (Sutherland 1981).

With increasing depth, annual changes in species abundance are fewer (Karlson 1978). Much space is occupied by relatively long-lived organisms such as the hydroid Hydractinia echinata, the sponge Xestospongia halichondroides, the anemone Diadumene leucolena (Karlson 1978), and the coral Oculina arbusculum (McCloskey 1970).

In the South Atlantic Bight near Cape Canaveral, FL, annual changes in species abundance are fewer even in shallow water assemblages (Mook 1976, 1980, 1981, 1983b). Balanus spp. and the tube building amphipod Corophium lacustre dominate these communities throughout the year.

Patterns of Recruitment

When substrate has been experimentally cleared (Ortega 1981) or when new jetties are constructed (Van Dolah et al. 1984), the general pattern of intertidal zonation is restored or created by recruitment within a year. Near Beaufort, NC, Ortega (1981) reports most intertidal recruitment of Balanus spp. during summer and of Crassostrea virginica and Brachidontes exustus in fall, but it is unknown whether this pattern is typical for the Atlantic Bight. Recruitment of oysters is much higher in protected waters than on jetties and pilings on the open coast, while the reverse is true for mussels (Ortega 1981). It is likely that recruitment is lowest from January to March when temperatures are minimal (e.g. Sutherland and Karlson 1977).

Most studies of recruitment patterns of subtidal, sessile animals (fouling organisms) have been conducted in North Carolina (McDougall 1943; Maturo 1959; Wells et al. 1964; Sutherland and Karlson 1977; Sutherland 1981). The most extensive study is that of Sutherland (Sutherland and Karlson 1977, Sutherland 1981) who collected data at Beaufort, NC, for 6 1/2 years (Figure 15). Periods of recruitment for 11 common species show considerable seasonality because of the wide annual temperature range at Beaufort. Some species, such as Haliclona, Halichondria, Tubularia, Halocordyle (=Pennaria), and Botryllus, recruited only periodically. Others recruited predictably each year (e.g., Schizoporella, Styela, Ascidia, and Crassostrea) while still others (e.g., Bugula and Balanus spp.) recruited almost continuously (Figure 15). In any given year recruitment could be extremely variable from month to month, resulting in different patterns of community development on newly submerged substrate (Sutherland and Karlson 1977).

Just south of Cape Canaveral, FL, similar variation in patterns of recruitment has been observed by Mook (1976, 1980, 1983b) even though the annual fluctuation in temperature there is less. Some species recruited only periodically, some predictably each year, and some almost continuously. Organisms that were common throughout the South Atlantic Bight tended to recruit more continuously throughout the year (Mook 1976, 1980). Organisms with more tropical affinities recruited primarily during the warmer months.

3.4 FISHES

Community Composition

The coastal warm-temperate fishes of the South Atlantic Bight fluctuate seasonally in species composition and abundance (Huntsman and Manooch 1978; Miller and Richards 1979; Lindquist et al. 1985; Van Dolah et al. 1986). Most coastal fishes are absent in winter and gradually return to inshore habitats as waters warm in spring. Fishes found on coastal jetties tend to be a subset of those found on inshore oyster reefs and offshore hard bottoms. These fishes can be grouped into five general categories based on their mobility, need for benthic habitat complexity, and seasonality of jetty occupancy. The first group consists of a limited number of small cryptic species, such as those in the blenny (Blenniidae) and goby (Gobiidae) families that generally do not move over large distances and are dependent upon the structural complexity of the jetties. These fishes are often resident year-round. The second group consists of a large number of numerically dominant species such as pinfish, Lagodon rhomboides, spottail pinfish, Diplodus holbrooki, black sea bass, Centropristis striata, and pigfish, Orthopristis chrysoptera, that are abundant during warmer months but move offshore in cold winter months. The third group is made up

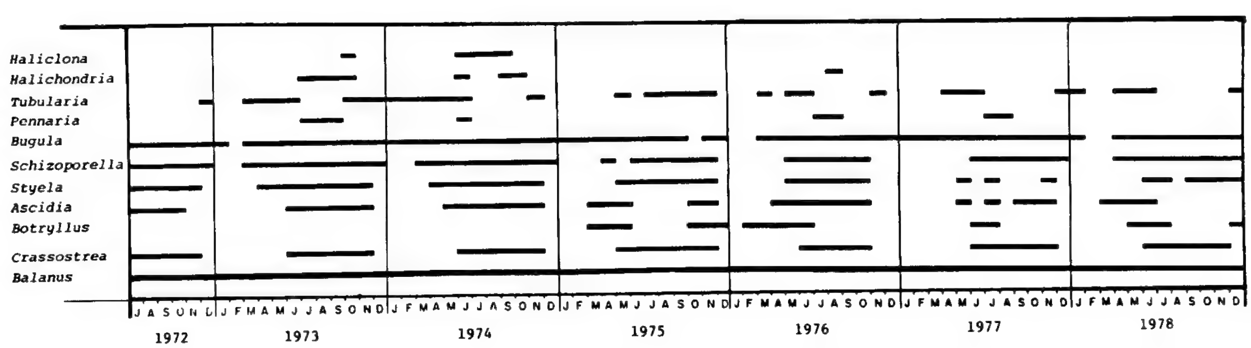


Figure 15. Recruitment periodicities for 11 common invertebrate species. Bars indicate when recruitment was observed on artificial plates exposed for 1-4 weeks (Sutherland 1981).

of several large predatory species such as bluefish, Pomatomus saltatrix, and Spanish mackerel, Scomberomorus maculatus, that move over large distances but are attracted to jetties because of the increased density of prey that occurs there. The fourth group contains species, like the smooth dogfish, Mustelus canis, that are attracted to jetties during their northerly migration in spring or their southerly migration in fall (Van Dolah et al. 1984, 1986). The fifth and least important group contains various tropical fishes (e.g., butterflyfishes of the family Chaetodontidae and surgeonfishes of the family Acanthuridae) that occur as strays during the warmest months of the year. Only fishes in the first and second groups are truly residents of rubble structures.

Although the fishes of the South Atlantic Bight are well known (Bohlke and Chaplin 1968; Dahlberg 1975; Manooch 1984; Robins et al. 1986), very few studies have focused specifically on the fishes using nearshore rubble structures. Van Dolah et al. (1984, 1986) conducted extensive investigations of the fishes associated with the large jetties at Murrells Inlet, SC, and Lindquist et al. (1985) studied those on smaller jetties at Masonboro Inlet, NC. Data collected by Van Dolah et al. (1984, 1986) are the most extensive presently available and the patterns they document agree well with those seen on offshore artificial reefs (Parker et al. 1979; M. Hay, pers. obser.). We consider their findings to be broadly representative of the patterns that occur on most jetties in the South Atlantic Bight. During their investigations at the Murrells Inlet site, Van Dolah et al. (1984, 1986) collected 93 species of fishes representing 43 families. A few of the most common species are discussed below. For illustrations and species descriptions of all the fishes discussed in this text, see Robins et al. (1986).

The smooth dogfish, Mustelus canis, and the clearnose skate, Raja eglanteria, are often abundant near jetties during the spring when they are migrating from deeper to shallower waters or from southern to more northerly waters. The clearnose skate is the most common species of skate in inshore waters between Long Island and North Carolina and grows to have a disc width of slightly less than 1 m (Robins et al. 1986). It feeds primarily on fishes and larger crustaceans (Hildebrand and Schroeder 1928; Van Dolah et al. 1986) and, as its name suggests, has broad clear areas on each side of the snout. The smooth dogfish is a small (up to 1.5 m in length) shark that occurs between the Bay of Fundy and Uruguay. It has several rows of small, pavement-like teeth and, like the clearnose skate, feeds on larger crustaceans and small fishes (Hildebrand and Schroeder 1928; Van Dolah et al. 1986).

Bluefish, Pomatomus saltatrix, are found between Nova Scotia and Argentina, although they are rare or absent in the Caribbean. During the spring and summer, they are common in coastal areas along the South Atlantic Bight. These large (up to 1.1 m in length and 12 kg in mass) predators form aggregations when actively feeding that often drive schools of prey fishes into shallow waters near swimming beaches. On such occasions, swimmers and surfers have been bitten. Although bluefish are not resident on jetties, they often feed on the fishes that do reside there and are often caught by anglers casting from jetties. Bluefish are primarily piscivorous but may also consume nereid worms, crustaceans, and cephalopods (primarily squids) (Hildebrand and Schroeder 1928; Grant 1962; Richards 1976; Gallaway et al. 1981; Van Dolah et al. 1986).

Other common piscivores are the Spanish mackerel, Scomberomorus maculatus, and the conger eel, Conger oceanicus. Like bluefish, Spanish mackerel move widely between many habitats but frequent jetties to feed on resident jetty fishes. They attain lengths greater than 80 cm, weigh up to 5 kg, and can be distinguished from most other mackerel by the many large, dark brown and brassy spots on their sides. The conger eel is dark brown to bluish gray, grows to a size of 2.3 m and 40 kg. It is often caught by anglers fishing on jetties, docks, or piers in the mid-Atlantic States (Robins et al. 1986). Spanish mackerel and conger eels occur between Cape Cod and the Gulf of Mexico.

Three sparid fishes are common on rubble structures in the South Atlantic Bight: the pinfish, Lagodon rhomboides, the spottail pinfish, Diplodus holbrooki, and the sheepshead, Archosargus probatocephalus. Darcy (1985a, b) reviewed available information on pinfish and spottail pinfish, and Ogburn (1984) investigated feeding by sheepshead on a North Carolina jetty. Despite the common perception that herbivorous fishes are absent from temperate communities (Bakus 1964, 1968; Montgomery 1977, 1980; Ogden and Lobel 1978; Montgomery and Gerking 1980; Hay 1981b; Gaines and Lubchenco 1982), all three of these species can consume large quantities of seaweeds (Carr and Adams 1973; Adams 1976a; Stoner 1980; Ogburn 1984; Stoner and Livingston 1984; Hay 1986; Hay et al. 1987, 1988) and may significantly affect the structure of benthic seaweed communities (see later sections). In addition to seaweeds, sheepshead may consume significant quantities of bivalves and barnacles (Parker et al. 1979; Van Dolah et al. 1984). In the Carolinas, spottail pinfish and pinfish are among the most abundant species on jetties. Sheepshead are common but much less abundant (Lindquist et al. 1985; Hay 1986; Van Dolah et al. 1986).

Individuals of all of these species tend to be relatively small on coastal rubble structures compared to the larger individuals that occur on offshore reefs. Young individuals appear to colonize jetties in early spring, grow rapidly throughout the summer, and move to deeper offshore areas as nearshore waters cool in the late fall (Darcy 1985a, b; Lindquist et al. 1985; Van Dolah et al. 1986). In the Carolinas, these fishes are among the major prey species on offshore reefs. Their inshore-to-offshore migrations may be important in transferring energy between productive inshore and deeper offshore habitats (Darcy 1985a, b). Pinfish occur between Cape Cod and the Yucatan. Spottail pinfish are found between the Chesapeake Bay and the northern Gulf of Mexico. Sheepshead are more widely distributed and occur from Nova Scotia to Brazil (Robins et al. 1986).

Pigfish, Orthopristis chrysoptera, show seasonality and migratory patterns that resemble those of the sparids discussed above. Near Beaufort, NC, offshore migration occurs in late fall or winter. The largest individuals are the first to leave and the first to return in the spring (Hildebrand and Cable 1930). Since individuals returning in the spring appear to be in poor condition due to the less than optimal feeding conditions offshore, pigfish probably migrate to avoid low temperatures rather than to seek better feeding grounds (Darcy 1983). Pigfish are attracted to hard substrate and often school near reefs or jetties (Hastings 1972). They are generalist carnivores, with prey size and type changing as a function of age (Hildebrand and Cable 1930; Carr and Adams 1973). Small fish feed on planktonic crustaceans. Larger fish feed on small fishes, benthic crustaceans, mollusks, polychaetes, and a variety of other invertebrates. Pigfish occur from Massachusetts to the Yucatan.

Spot, Leiostomus xanthurus, are popular panfish common on jetties during the spring and fall. They are found between Massachusetts and the northern Gulf of Mexico, and eat primarily bivalves, decapods, and smaller crustaceans (Adams 1976a; Van Dolah et al. 1986).

Both black sea bass, Centropristis striata, and tautog, Tautoga onitis, are abundant predators that reside on coastal jetties. Black sea bass range from Maine to the northern Gulf of Mexico. Tautog occur as far north as Nova Scotia but extend southward only to Georgia (Robins et al. 1986; Gilligan 1987). Both of these species are commonly taken by hook and line and by spear. Lindquist et al. (1985) and Van Dolah et al. (1986) found that tautog consumed primarily jetty-associated bivalves and crustaceans. Black sea bass also consume considerable quantities of crustaceans, but the major portion of their diet is fish and they rarely consume bivalves. Juvenile black sea bass eat a mixed diet of fish, decapods, amphipods, and other benthic invertebrates. As black sea bass increase in size, the proportion of fish in the diet increases consistently (Van Dolah et al. 1986).

Oyster toadfish, _Opsanus tau_, skilletfish, _Gobiesox strumosus_, seaboard gobies, _Gobiosoma ginsburgi_, crested blennies, _Hypleurochilus geminatus_, and feather blennies, _Hypsoblennius hentzi_, were all common on the South Carolina jetties studied by Van Dolah et al. (1986). These fishes are cryptic and tend to be less mobile, and thus less seasonal, than the other fishes common on rubble structures in the South Atlantic Bight. They appear to be among the only fishes that overwinter on the jetties and that do not migrate seasonally to warmer waters. Winter densities of these fishes appear to be lower than densities in warmer months. However, this could be a sampling artifact since most blennies and gobies become inactive and shelter in crevices at low water temperatures. This behavior would increase their probability of being undersampled during the winter.

On the jetties studied by Van Dolah et al. (1986), oyster toadfish ate primarily fishes (Atlantic silverside, _Menidia menidia_, menhaden, _Brevoortia tyrannus_, and black sea bass) and decapods. Skilletfish, blennies, and seaboard gobies consumed a diet of mixed invertebrates.

The skilletfish is the only clingfish on the U.S. coast that occurs north of Florida, its range extending from New Jersey to Brazil. Oyster toadfish occur between Cape Cod and Florida. Because of their size and hardiness (ability to withstand pollution and other stresses), they have become important experimental and bioassay organisms. Seaboard gobies occur from Massachusetts to Georgia, feather blennies from New Jersey to Texas, and crested blennies from North Carolina to Texas (Robins et al. 1986).

Large schools of Atlantic silversides, _Menidia menidia_, sometimes aggregate over shallow portions of jetties and consume the epifaunal amphipods that occur there (Van Dolah et al. 1986). Since Atlantic silversides are typically found along sandy shore lines and at the mouths of inlets, their occasional association with jetties is more likely explained by the location of jetties at inlet mouths than by their attraction to the jetties themselves. Atlantic silversides occur from the Gulf of St. Lawrence to the northeastern coast of Florida (Robins et al. 1986). In addition to epifaunal amphipods, they consume other small benthic and planktonic crustaceans, polychaetes, bivalves, and juvenile fishes (Hildebrand and Schroeder 1928; Adams 1976a; Bengston 1984; Van Dolah et al. 1986).

Distribution

The species composition of large, noncryptic fishes on shallow rubble structures is similar to the community composition seen on natural and artificial reefs that occur offshore in the South Atlantic Bight (Parker et al. 1979; Van Dolah et al. 1984; Sedberry and Van Dolah 1984; Lindquist et al. 1985; Van Dolah et al. 1986). However, inshore jetties tend to have a lower diversity of species than natural, offshore reefs. Also the size of individual fishes tends to be smaller on jetties (Buchanan 1973; Van Dolah et al. 1986; Wenner et al 1986), suggesting their role as nurseries.

When rubble structures such as jetties are constructed, they are very rapidly colonized by fishes. The seasonal nature of the inshore fish fauna obscures successional patterns in fish community structure on new jetties, if such patterns occur (Hastings 1979; Van Dolah et al. 1984; Lindquist et al. 1985). The rapid movement of fishes onto newly constructed jetties suggests that they are initially attracted by the increased structural complexity, which provides shelter from predators. However, gut content analyses of common jetty fishes such as black sea bass, pinfish, spottail pinfish, sheepshead, spadefish (_Chaetodipterus faber_), tautog, grunts (Haemulidae), and flounder (Bothidae) show that they soon come to rely on jetty-associated fauna as a food source (Ogburn 1984; Van Dolah et al. 1984, 1986; Lindquist et al. 1985). When Lindquist et al. (1985) compared the fishes associated with a new jetty (1 year old) to an older one (15 years old) at Masonboro Inlet, NC, they found few significant differences in species' densities. Pigfish and sheepshead were more abundant on the new jetty but it is possible that differences other than jetty age caused these patterns. On North

Carolina jetties, differences in fish populations on old versus new jetties and on ocean versus inlet sides of jetties appear to be small compared to the major differences in spatial use patterns observed over depth gradients (Lindquist et al. 1985). Of the nine abundant species studied by Lindquist et al., six were significantly more abundant at a depth of 2 m than at 4 m (pinfish, spottail pinfish, sheepshead, pigfish, bluefish, and round scad, Decapterus punctatus), one was more abundant at 4 m (black sea bass), and two showed no significant changes in abundance between these depths (tautog and spot). Van Dolah et al. (1986) noted similar patterns for several of these species on the South Carolina jetties they studied; our experience with the North Carolina jetties at Cape Lookout, Shackleford Banks, and Radio Island suggests that these patterns occur on those jetties as well.

The abundance of sparid fishes (pinfish, spottail pinfish, and sheepshead) is known to be positively correlated with vegetation cover. Stoner (1980b) demonstrated a very high correlation ($r = 0.998$, $p < 0.01$) between pinfish abundance and macrophyte biomass in seagrass beds. Other authors have made similar observations (Caldwell 1957; Kilby 1955; Schwartz 1964). It appears that the sparids are abundant in shallow areas because of the increased abundance of seaweeds. Seaweeds are fed on directly and also support populations of small crustaceans that are another important component of the sparid diet (Ogburn 1984; Darcy 1985a, b). Pelagic sport fishes, such as bluefish and spanish mackerel, may be attracted to these shallower depths because of the increased abundance of sparids and other prey.

As mentioned earlier, large seasonal changes occur in the species composition and abundance of fishes on rubble structures in the South Atlantic Bight. Numerous studies suggest that most of these changes are driven by the need of fishes to avoid the colder inshore water temperatures that occur in winter (Huntsman and Manooch 1978; Miller and Richards 1979; Parker et al. 1979; Lindquist et al. 1985; Van Dolah et al. 1986). Even though these seasonal temperature changes are less pronounced at lower latitudes, the same general patterns of offshore or southerly migrations appear to occur throughout the entire South Atlantic Bight. As an example, pinfish and spottail pinfish undergo similar patterns of seasonal migration in both North Carolina and Florida (Adams 1976b; Stoner and Livingston 1984; Darcy 1985a, b).

Seasonal patterns of abundance on jetties in the bight have been studied most extensively on the jetties at Murrells Inlet, SC (Van Dolah et al. 1984, 1986). Abundance and community composition of fishes frequenting these jetties were assessed quarterly using gill nets, visual observations, crab traps modified to retain small fishes (6.4 mm mesh), unmodified crab traps, and qualitative rotenone collections. Gill nets were run from the jetty to a distance of 23 m away from the jetty to sample not only resident jetty fishes, but also pelagic predators preying on these fishes. Crab traps were deployed on, or very near, the jetties and thus assessed jetty fishes that would enter traps. Visual counts by divers provided an additional assessment of noncryptic jetty fishes that may not have been adequately sampled by the other techniques. The qualitative rotenone collections allowed a crude assessment of small cryptic species like blennies and gobies. Rotenone is a toxin that stresses small fish, causing them to leave their cryptic habitats and swim into the open water where they can be collected.

Data from these studies are shown in Table 1 and in Figures 16-25. Most of these data are reported in the literature, and thus in our tables and figures, without an indication of the variance (Van Dolah et al. 1984, 1986). We have included measurements of variance where they exist. The only other available studies dealing with fishes on jetties in the bight (Ogburn 1984; Lindquist et al. 1985; Hay 1986) are less extensive but show similar patterns.

The total number of fish species seen in visual counts, or collected using gill nets or modified crab traps, was highest during warmer seasons of the year and decreased markedly in winter (Table 1).

Table 1. Number of fish species collected or counted during different seasons on the jetties at Murrells Inlet, SC (data from Van Dolah et al. 1986).

Method	Spring	Summer	Fall	Winter
Visual transects	11	24	22	1
Gill nets	25	34	25	6
Modified crab traps	7	5	3	2
Unmodified crab traps	11	9	8	7
Rotenone	13	11	12	9

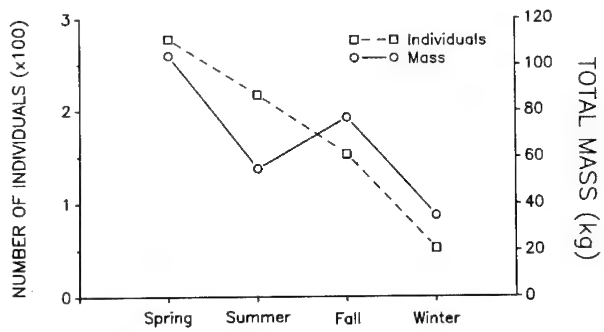


Figure 18. Unmodified crab trap collections from the north jetty at Murrells Inlet, SC. Plotted are the total number and mass of fishes collected during each season using 15 traps set for a period of 12 daytime and 12 nighttime hours during each season (data from Van Dolah et al. 1986).

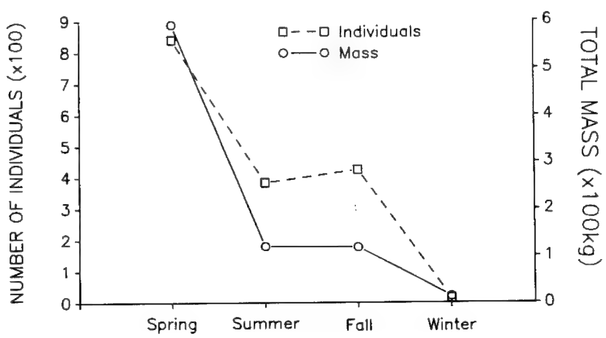


Figure 16. Gill net collections from jetties at Murrells Inlet, SC. Plotted are the totals from three nets deployed for 3-hour set periods during each season. One end of the 30.5 m long net was set on the jetty; the other end was about 23 m from the jetty (data from Van Dolah et al. 1986).

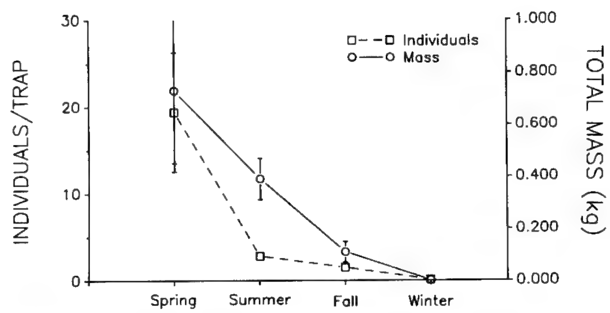


Figure 19. Modified crab trap (covered with 6.4 mm mesh to retain small fishes) collections from the base of jetties at Murrells Inlet, SC. Plots show means ± 1 standard error for 14 traps that were set for 3 hours during each season (data from Van Dolah et al. 1986).

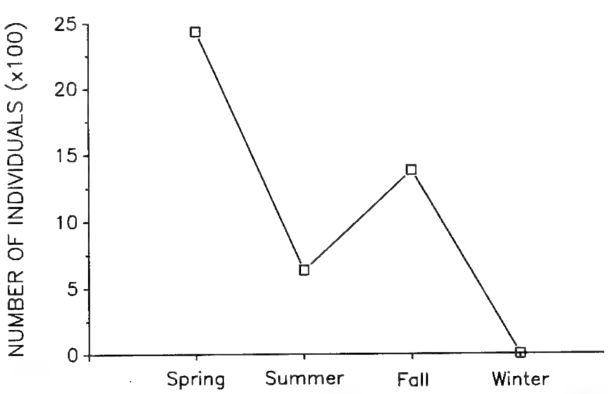


Figure 17. Diver observations of the seasonal abundance of common fishes on the jetties at Murrells Inlet, SC. Plotted are the totals from ten 5-min counts in each season (data from Van Dolah et al. 1986).

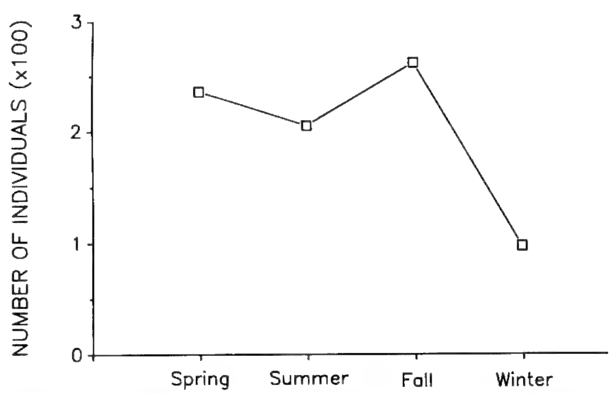


Figure 20. Rotenone collections from the jetties at Murrells Inlet, SC. Plotted are the total number of fishes in a single qualitative collection made during each season (data from Van Dolah et al. 1986).

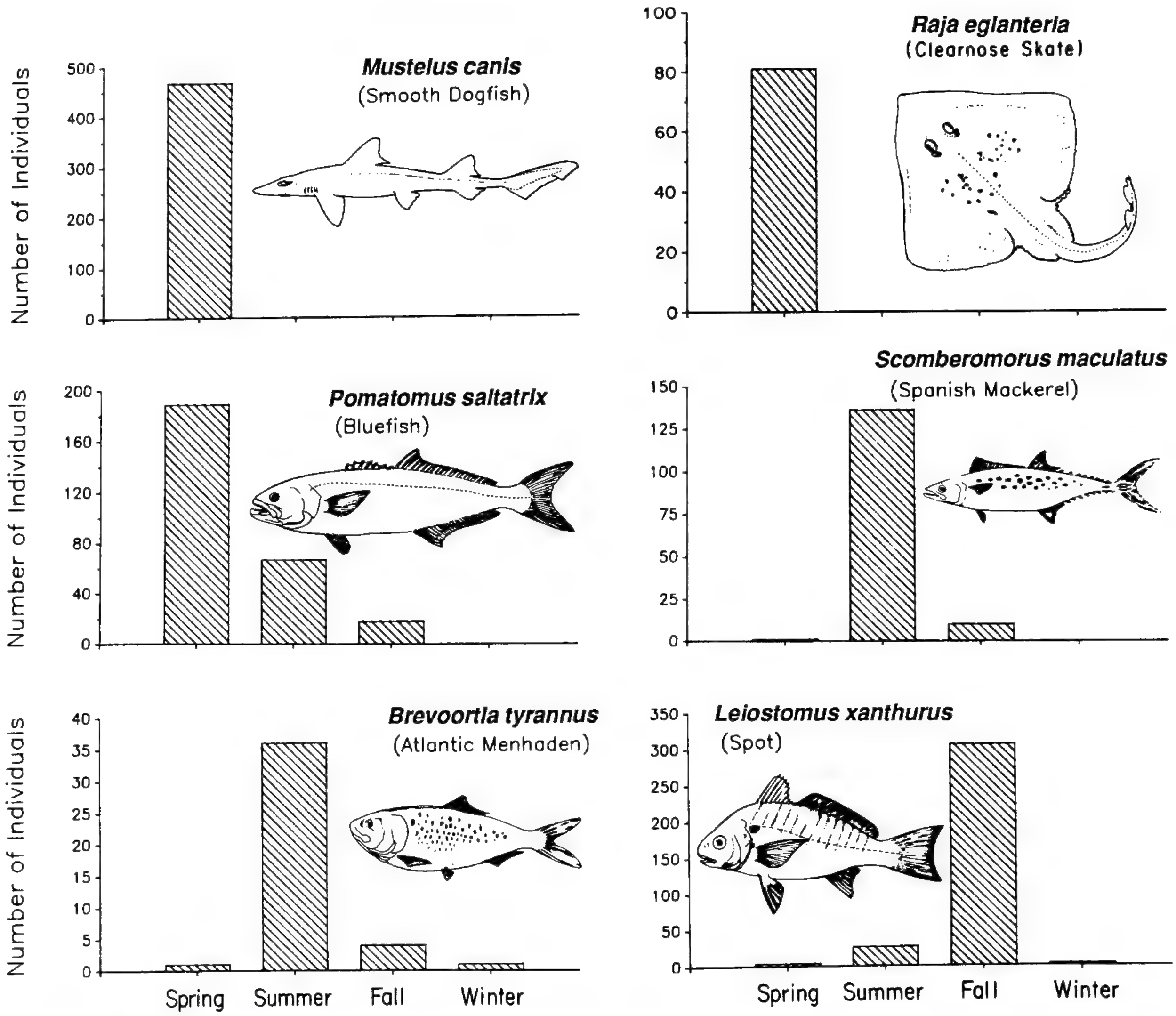


Figure 21. Seasonal abundance of common fishes captured in gill nets set near jetties at Murrells Inlet, SC. Histograms show the totals from 3 nets set for 3 hours during each season (data from Van Dolah et al. 1986).

Lindquist et al. (1985) also found a significant correlation between the mean number of species observed each month (counted in visual transects) and water temperature ($r = 0.82$, $p < 0.01$). Van Dolah et al.'s (1986) collections from unmodified crab traps and by rotenone indicated that species number was at a low in the winter, but the relative change was slight compared to that of the other collection methods (Table 1). Figures 16-20 show seasonal change in the total number, and in some cases total mass, of fishes collected by each method. All of these show large decreases in the winter even though unmodified crab traps and rotenone collections, again, tended to show smaller relative reductions than did the other collection methods. Rotenone collections focused primarily on small blennies and gobies that are probably less able than the larger species to successfully make the long offshore migration to deeper water. Reasons for the reduced seasonal variation in unmodified crab-trap collections are less apparent.

Figures 21-25 show seasonal patterns of abundance for the most common species

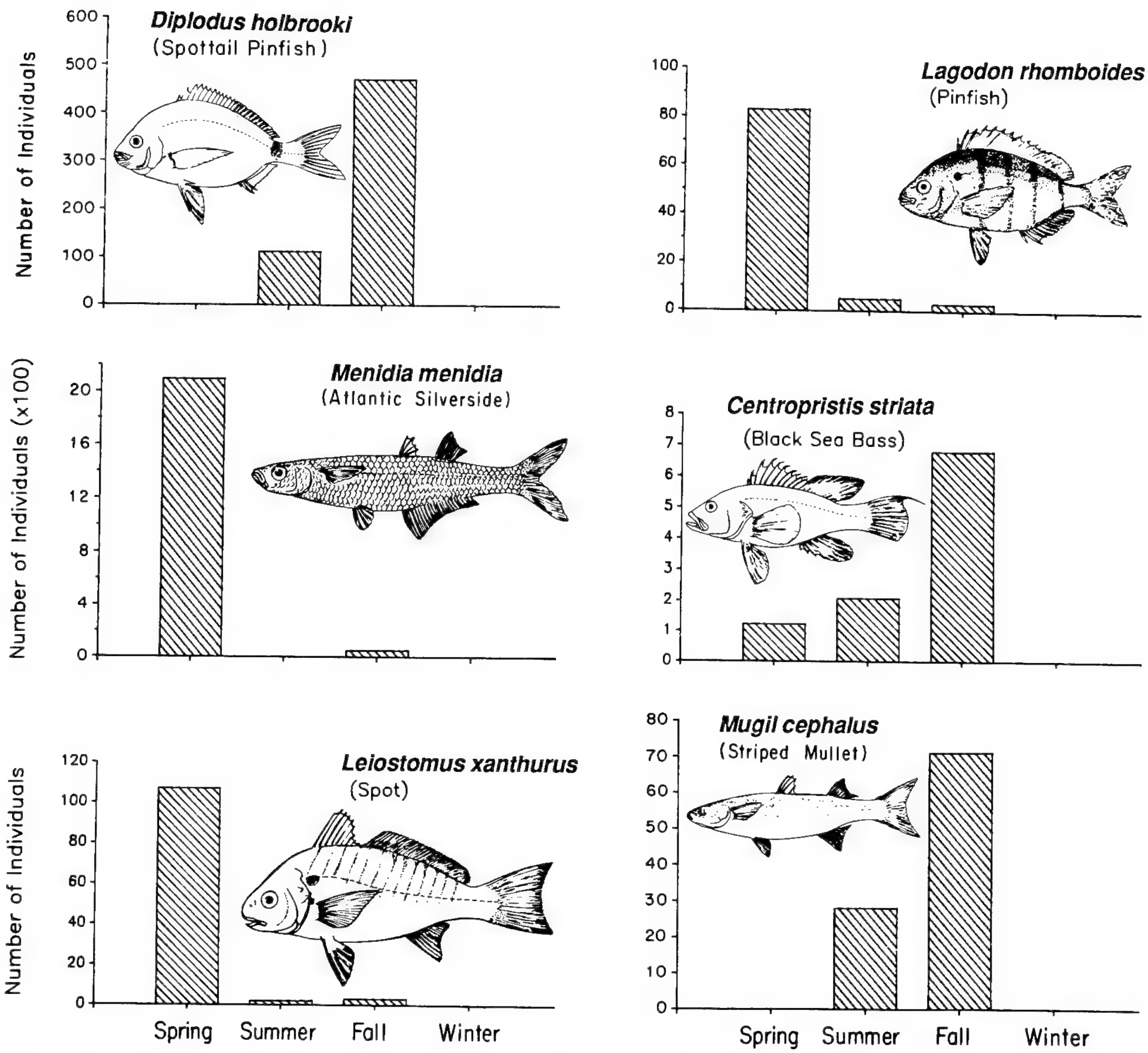


Figure 22. Seasonal abundance of common fishes observed by divers on the jetties at Murrells Inlet, SC. Histograms show the totals from ten 5-min counts during each season (data from Van Dolah et al. 1986).

assessed by each of the methods discussed above. All species show peak abundances in spring, summer, or fall and are absent or relatively rare in winter.

Feeding Patterns of Fishes On and Near Jetties

Three studies have investigated feeding by fishes on jetties in the South Atlantic Bight. Ogburn (1984) quantified the gut contents of sheepshead collected from jetties at Masonboro Inlet, NC, and Lindquist et al. (1985) investigated feeding by sheepshead, pinfish, spottail pinfish, and tautog on this same jetty. Van Dolah et al. (1986) have provided the broadest data base on this topic. They quantified the gut contents of 55 fish species captured near Murrells Inlet, SC. Table 2 shows their findings for those species and seasons where at least three individuals that contained food were examined. About half of the species examined fed primarily on jetty biota during one or more seasons. Sheepshead,

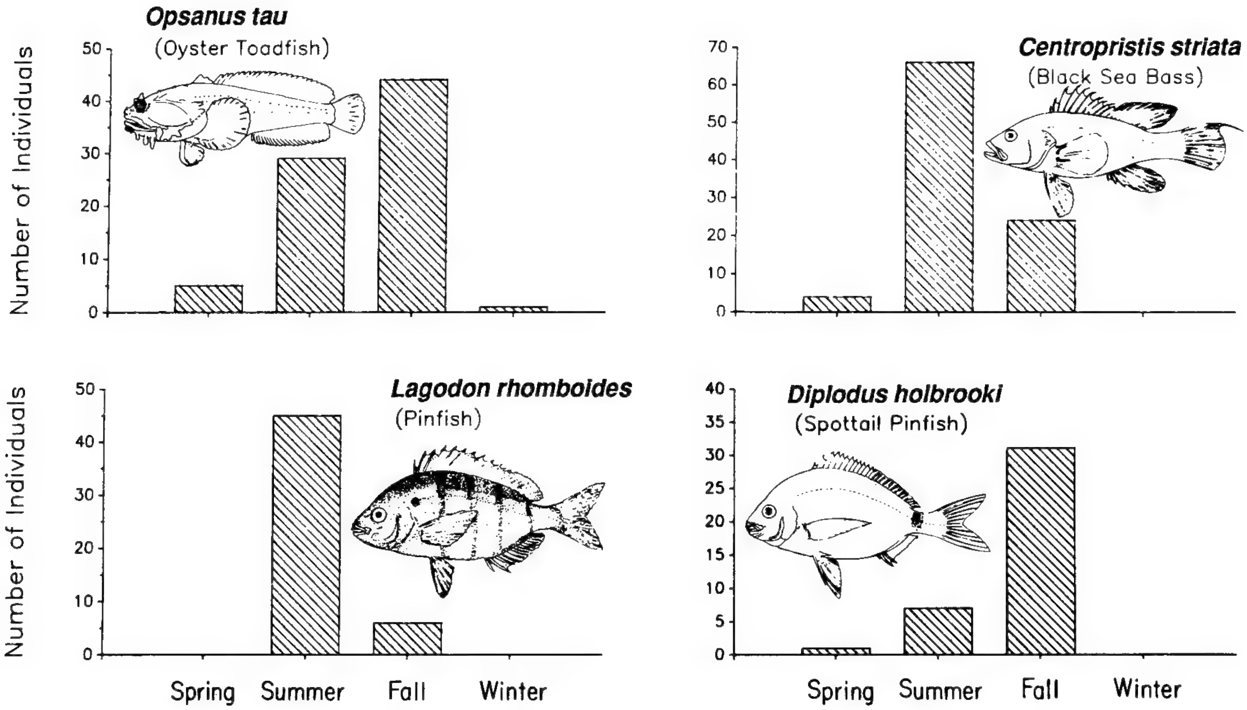


Figure 23. Seasonal abundance of common fishes captured in unmodified crab traps deployed on the north jetty at Murrells Inlet, SC. Histograms show the totals from 15 traps set for 12 hours during the day and 12 hours during the night for each season (data from Van Dolah et al. 1986).

black drum (Pogonias cromis), tautog, and spadefish were among the important recreational fishes that fed almost exclusively on jetty biota. Other important recreational fishes, such as bluefish, black sea bass, spotted seatrout (Cynoscion nebolosus), red drum (Sciaenops ocellatus), Spanish mackerel, and weakfish (Cynoscion regalis), were indirectly dependent on the jetty since they fed heavily on smaller fishes that directly consumed jetty biota (Van Dolah et al. 1986).

Patterns of Recruitment

The general pattern of larval recruitment seen for most reef fishes in the South Atlantic Bight is that large numbers of juveniles invade reefs, jetties, or estuaries starting late in the winter and continuing throughout the summer (Hildebrand and Cable 1930; Wang and Raney 1971; Hoss 1974; Thayer et al. 1974; Adams 1976b; Parker et al. 1979; Bozeman and Dean 1980; Van Dolah et al. 1986). In our experience with jetties in North Carolina, it appears that jetties on the outer coast are colonized in the spring by both adults and juveniles, while jetties in the sounds are colonized primarily by juveniles.

Jetties as Concentrated Nurseries

Jetties often harbor high densities of young fishes that typically live on offshore reefs as adults. Pinfish, spottail pinfish, black sea bass, sheepshead, spadefish, and gag (Mycteroperca microlepis) all provide examples of this. For these fishes jetties obviously serve as nurseries, providing both feeding sites and the structural complexity necessary for avoiding predators. These fishes can be very dense on jetties (Figure 26); spottail pinfish can occur at $8/m^2$ (Hay 1986). However, the extremely small area covered by rubble structures compared to the immense stretches of sandy beaches and estuarine habitats in the bight, suggests that rubble structures cannot be having a

Table 2. The gut contents (% volume) of fishes collected on, or near, the jetties at Murrells Inlet, SC. Data are from Van Dolah et al. (1986). Included are those species and seasons in which at least three individuals containing food were examined.

Consumer (common name)	Size range (mm); SL=Standard length TL=Total length FL=Fork length DW=disc width	Stomachs with food/Stomachs examined	Season	Algae	Foraminiferida	Porifera	Hydrozoa	Anthozoa	Gastropoda	Bivalvia	Cephalopoda	Polychaeta	Pycnogonida	Ostracoda	Copepoda	Cirripedia	Stomatopoda	Decapoda	Mysidacea	Cumacea	Isopoda	Amphipoda	Insecta	Sipuncula	Bryozoa	Ophiuroidea	Echinoidea	Ascidiacea	Pisces	Other references to feeding See code below
Mustelus canis	590/980	25/25	SP							<1	<1	1					21	61											16	1
(smooth dogfish)	(TL)																													
Sphyrna tiburo	545-924	3/3	SP														81	4											15	1
(bonnethead shark)	(TL)	3/3	SU														5	95												
Raja eglanteria	248-615	25/25	SP														5	17	1										77	1
(clearnose skate)	(DW)																													
Dasyatis americana	325-585	3/3	SP									16						3	1			6							74	2,50-52
(southern stingray)	(DW)																													
Myliobatis freminvillei	307-480	11/12	SP						54									46												1
(bullnose ray)	(DW)																													
Opisthonema oglinum	156-168	3/4	SU									96			<1			<1											3	1,3,50
(three thread herrings)	(FL)																													
Arius felis	227-288	3/3	SU								73					<1	9	4											13	2,4,5
(hardhead catfish)	(SL)																													
Opsanus tau	150-280	6/9	SP	<1			<1			<1						<1		52				<1			<1	2			45	1,53
(oyster toadfish)	(TL)	15/18	SU	<1			<1			<1		<1						5							<1				94	
Gobiesox strumosus	15-74	9/11	SP	<1			<1		19	<1				<1	<1	6					19	51			3					1,5
(skilletfish)	(TL)	20/24	SU							25					<1			43			25	1							6	
		18/24	F							2						<1					92	5								
		9/13	W				2			4						4				2	54	36								
Hyporhamphus unifasciatus	133-215	24/25	SU	13			<1			2		1			26	12	<1	12			2	33								1
(halfbeak)	(SL)	12/24	F	8												1		66			<1	1	24							
Strongylura marina	284-460	14/26	SU								3	<1																	97	1,3
(Atlantic needlefish)	(SL)	12/29	F															<1											100	
Menidia menidia	74-90	25/25	SP							<1		3			6	<1		2	<1			81							8	1,6,7
(Atlantic silversides)	(SL)																													
Syngnathus fuscus	107-140	8/26	SP												28							69			3					1,6
(northern pipefish)	(TL)																													
Centropristis striata	71-218	25/25	SP	1			<1		<1	<1		8			<1			38	2		<1	12		<1	<1			6	33	8
(black sea bass)	(SL)	25/25	SU	<1			<1	6	<1	<1		<1						21	<1		<1	<1			<1	3			70	
		25/25	F	<1			1		<1	<1		<1						29			<1	5				3		6	54[a]	
Pomatomus saltatrix	182-383	40/40	SP																										100	1,9-11
(bluefish)	(FL)	25/25	SU									8					<1	6											86	
		7/18	F																										100	
Selene vomer	107-218	3/3	SU																1										99	1
(lookdown)	(FL)	3/5	F															64											35	
Orthopristis chrysoptera	56-246	7/7	SU	<1					2	4		85						8			<1	<1								1,3,6,12
(pigfish)	(TL)																													
Archosargus probatocephalus	100-430	6/9	F	47			8		<1	35			<1			10						2			<1					1,5,10,13-16
(sheepshead)	(SL)																													
Lagodon rhomboides	62-176	8/8	SP	1			3								<1			4				4							88	1-4, 6,14,18-21
(pinfish)	(SL)	12/14	SU	31			3			2						2		21	<1		<1	11			<1			6	25	
		9/9	F	2	<1	1	3			14		3						12			<1	65			<1	<1				

Cynoscion nebulosus (spotted seatrout)	250-350 (TL)	9/9	F	2	<1	1	3			14		3					12			<1	65		<1	<1				1-3,5,15,21-23
		17/18	SU								11						15										74	
		3/4	F																								100	
Cynoscion regalis (weakfish)	255-400 (TL)	5/8	SP																								100	24-26
		2/3	SU																								100	
		4/4	F																								100	
Leiostomus xanthurus (spot)	12-208 (SL)	18/20	SP									3			31		5	7			53							1,2,4,6,21,25-36
		19/26	SU						2	52		3			<1	3	16	15	<1	<1	7							
		23/25	F	<1			<1		2	41		<1					4	<1		5	47	<1	<1			<1		
		9/23	W							7					<1					9	83				<1			
Menticirrhus americanus (southern kingfish)	227-278 (SL)	3/3	F	5						<1							69										26	1,37
Menticirrhus littoralis (gulf kingfish)	239-368 (SL)	23/30	SP						<1		<1						99	<1			1							1,37
		6/6	SU							8							90	2			<1							
		11/16	F														100				<1							
Micropogonias undulatus (Atlantic croaker)	176-267 (SL)	4/7	SU														100	<1										2,4,18,21,23, 25-29,33-35,38,39
Pogonias cromis (black drum)	222-463 (SL)	6/8	SP	1			<1		<1	78		<1					21				<1							1,2,4,15,21,23
		3/3	SU						<1	76						<1	22	<1		1							<1	
		3/3	F	<1					<1	95		<1				<1	2			<1						2		
Sciaenops ocellatus (red drum)	242-262 (SL)	3/5	SU														33										67	1,2,5,22,40-43
Chaetodipterus faber (spadefish)	135-230 (SL)	6/6	SU	7		70	2	15					<1				<1			<1	2		1	<1		2		1,10,13,39,44,50
Tautoga onitis (tautog)	188-288 (SL)	4/4	SP	<1					<1	66		1					22				10		1					1,8,14,45
		5/6	SU	<1			<1			29		2				38	18			<1	<1		11					
Hypleurochilus geminatus (crested blenny)	26-79 (TL)	10/10	SP	3			7			2		4				1					81		1					10,46
		25/25	SU				48			8		1								7	1		11			24		
		25/25	F				49		<1	12		6	2	<1		7				9	12		1			2		
		14/16	W			1	45			5		4		<1	2	3	1			13	5		9			9		
Hypsoblennius hentzi (feather blenny)	19-62 (TL)	10/10	SP							1		12		1		31				7	48		1					1,46
		8/9	SU				6					53				37				2	1							
		25/25	F			1	6			2		<1				36	<1			10	40		2			2		
Gôbiosoma ginsburgi (seaboard goby)	12-42 (TL)	12/22	SP							7		2									89		2					1,47
		25/25	SU			1				15		16		3	23	1	6			7	25							
		25/25	F							36		4		8	4	1				10	38							
		25/25	W							8		19			7					20	50							
Scomberomorus maculatus (Spanish mackeral)	253-418 (FL)	25/25	SU																								100	48,49
Peprilus alepidotus (harvestfish)	125-154 (SL)	9/28	SP						17																		83	1

a Many of the black sea bass examined in fall were from traps baited with menhaden. This probably inflated the proportion of fish in the diet.

Code for feeding references:

1. Hildebrand & Schroder 1928
2. Darnell 1958
3. Carr & Adams 1973
4. Diener et al. 1974
5. Odum & Herald 1972
6. Adams 1976[a]
7. Bengston 1984
8. Steimle & Ogren 1982
9. Grant 1962
10. Gallaway et al. 1981
11. Richards 1976
12. Darcy 1983
13. Van Dolah et al. 1984
14. Lindquist et al. 1985
15. Overstreet & Heard 1982
16. Ogburn 1984
17. Springer & Woodburn 1960
18. Hansen 1969
19. Stoner 1980[a]
20. Darcy 1985[a]
21. Darnell 1961
22. Mercer 1984[a]
23. Pearson 1929
24. Merriner 1975
25. Chao & Musick 1977
26. Stickney et al. 1975
27. Currin et al. 1984
28. Govoni et al. 1983
29. Govoni et al. 1986
30. Hales & Van de Aryle 1985
31. Hodson et al 1981
32. Kjelson et al 1975
33. Kobylinski & Sheridan 1979
34. Roelofs 1954
35. Sheridan & Trim 1983
36. Smith et al. 1984
37. Bearden 1963
38. Overstreet & Heard 1978b
39. Reid et al. 1956
40. Bass & Avault 1975
41. Mercer 1984b
42. Overstreet & Heard 1978a
43. Boothby & Avault 1971
44. Randall & Hartman 1968
45. Olla et al. 1974
46. Lindquist & Dillaman 1986
47. Munroe & Lotspeich 1979
48. Naughton & Soloman 1981
49. Berrien & Finan 1978
50. Randall 1967
51. Bigelo & Schroeder 1953
52. Radcliffe 1914
53. Schwartz & Dutcher 1963

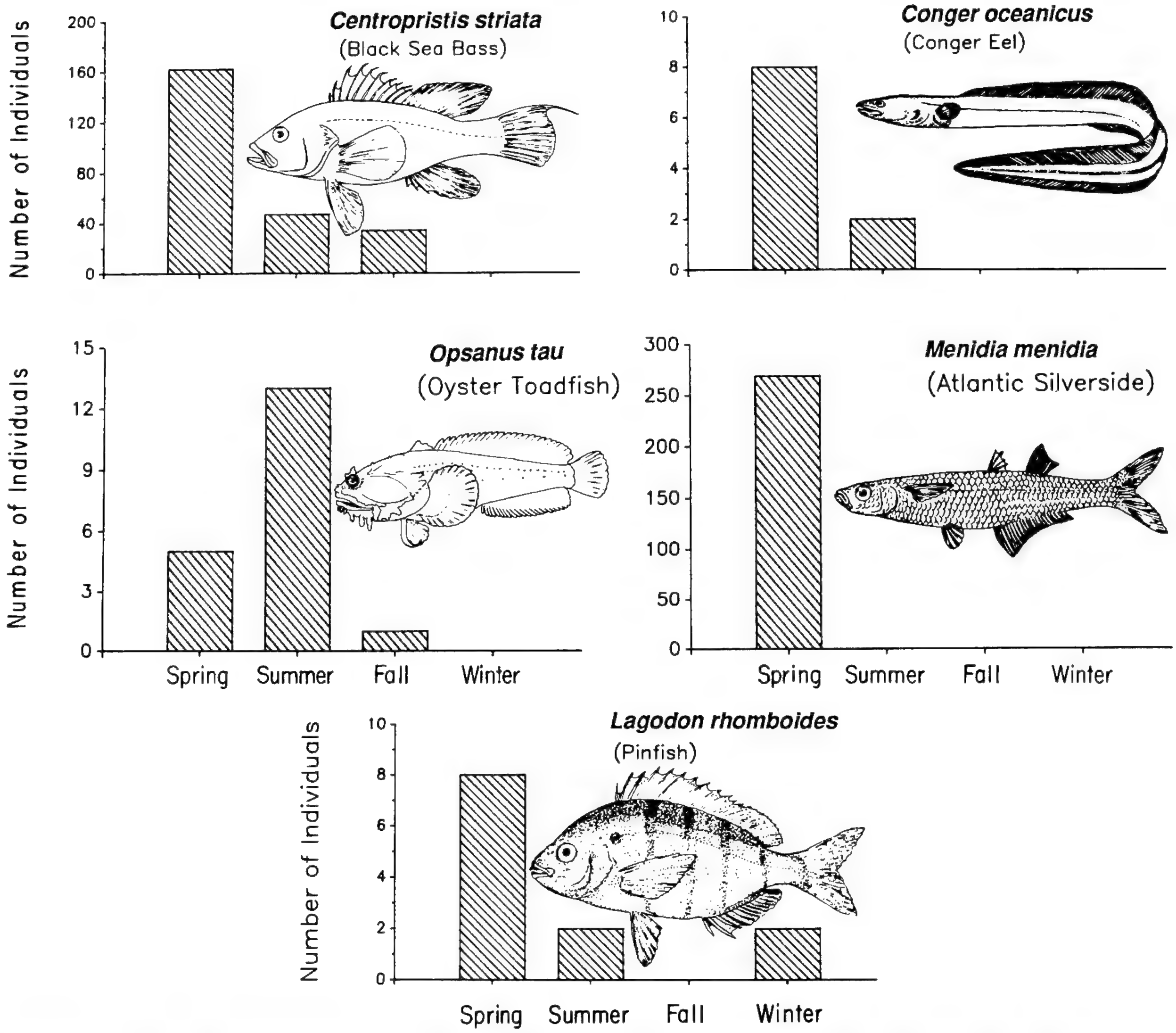


Figure 24. Seasonal abundance of common fishes captured in modified crab traps at Murrells Inlet, SC. Histograms show the total numbers captured in 24 traps set for 3 hours during each season (data from Van Dolah et al. 1986).

significant effect on the regional abundance of these species.

3.5 BIRDS

Community Composition

A great variety of birds in the South Atlantic Bight use rubble structures as loafing or roosting sites. However, birds in a few ecological categories, or "guilds", feed on or near jetties and can be considered part of the rubble structure community. The guilds include: (1) surface-searching shorebirds, (2) aerial-searching birds, (3) floating and diving water birds, and (4) wading birds (Table 3). Surface-searching shorebirds feed primarily on crustaceans, polychaetes, barnacles, molluscs, and insects. The most common shorebird is the ruddy turnstone, Arenaria interpres. When feeding on jetties it is often found in groups of 100 or more (C. Marsh; pers. comm.). Purple sandpipers, Calidris maritima, are also occasionally abundant, in flocks of 40-50. Both the ruddy

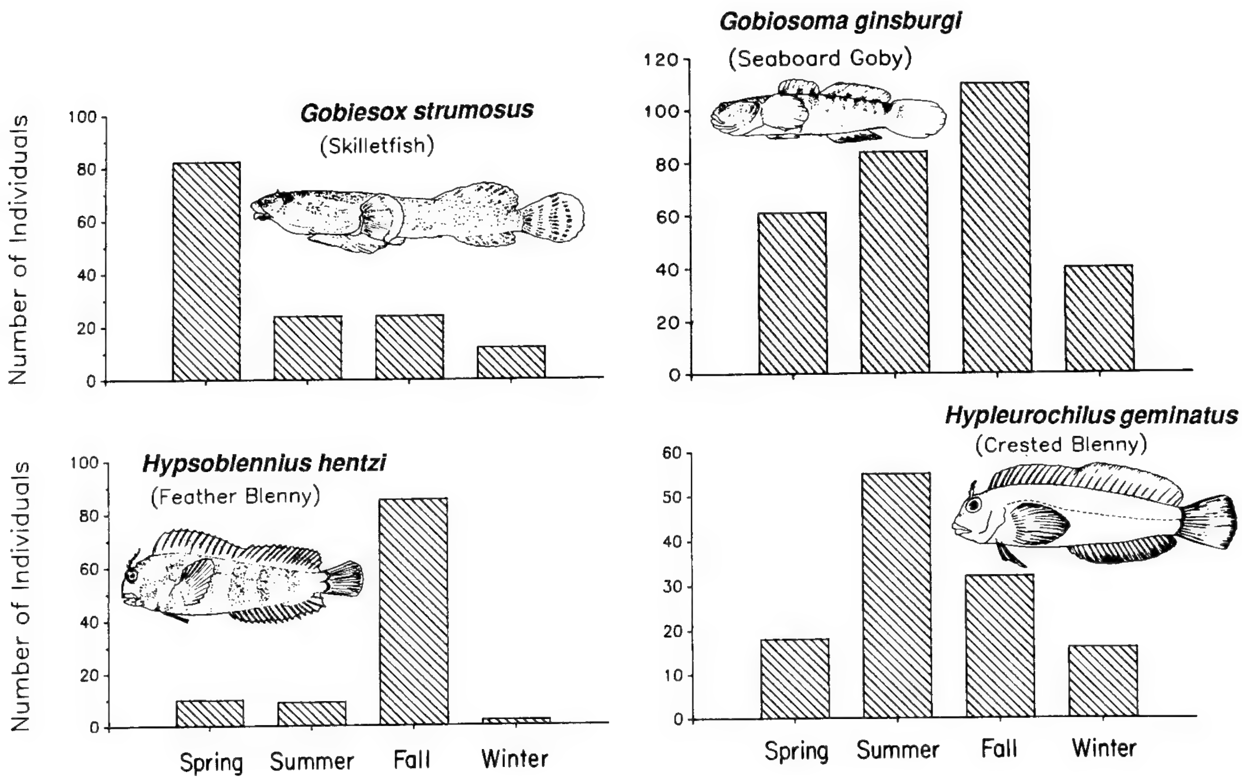


Figure 25. Seasonal abundance of common fishes in rotenone collections at Murrells Inlet, SC. A single collection was taken each season (data from Van Dolah et al. 1986).

turnstone and the purple sandpiper use rocks and jetties as their primary feeding habitats. Other shorebirds use them only on occasion, feeding on surrounding mudflats and seagrass beds as well (Peterson and Peterson 1978; Thayer et al. 1984).

Aerial-searching birds include a group of sea gulls (Table 3) which are opportunistic consumers of "anything they can get off the rocks" (C. Marsh; pers. comm.). This includes molluscs, crustaceans, fish, insects, carrion, and refuse. The most common bird in this group is the herring gull, Larus argentatus. Brown pelicans, Pelecanus occidentalis and a variety of terns are also frequently seen roosting on rubble structures, but generally do not use them as feeding sites (J. Parnell; pers. comm.).

The guild of floating and diving water birds is composed largely of a group of sea ducks (Table 3). Most of these are strong underwater swimmers and feed on echinoids (sand dollars) and bivalves (clams, and scallops) found on sandy bottoms near jetties. The surf scoter, Melanitta perspicillata, is a particularly capable diver, attaining depths of 12 m or more. Fish are also taken by birds in this group, especially by the double-breasted cormorant, Phalacrocorax auritus. The American wigeon, Anas americana, does not dive; it is a surface dabbler, feeding primarily on algae and seagrasses.

Wading birds (Table 3) are commonly found only near rubble structures built in estuaries away from severe wave action. In these quiet, shallow waters they can be seen feeding on small fishes and crabs.

Distribution

Most shorebirds that make use of jetties breed in the Arctic during June and July (Johnsgard 1981; Farrand 1983a).

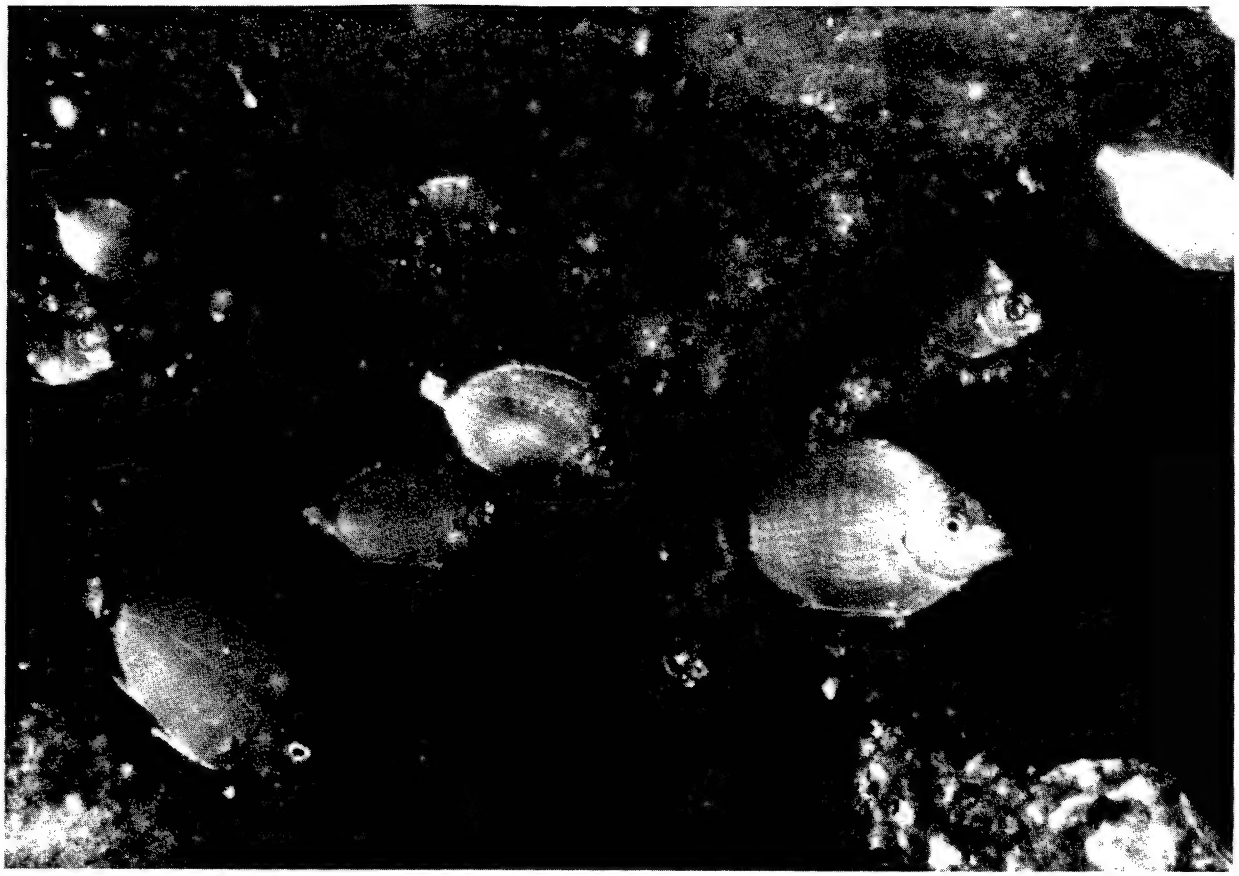


Figure 26. Spottail pinfish, *Diplodus holbrooki*, on the jetty at Radio Island, NC. The common sea urchin *Arbacia punctulata* can be seen in the lower center of the picture.

They can be found along the southeast coast of the United States during the rest of the year. The American oystercatcher and boat-tailed grackle are year-round residents. The ring-billed gull breeds in the western United States and Canada and is seen in the South Atlantic Bight only in winter. Other gulls are year-round residents (Farrand 1983b). Except for the double-breasted cormorant which is present year-round, most floating and diving water birds breed during the summer in Canada and the Arctic (Farrand 1983a). They can be found in the South Atlantic Bight during the remainder of the year. The wading birds are year-round residents.

Table 3. Types of birds common to rubble structures in the South Atlantic Bight.[a]

Species	Present
Surface-searching shorebirds	
Black-bellied plover (Pluvialis squatarola)	winter
Semipalmated plover (Charadrius semipalmatus	winter
American oystercatcher (Haematopus palliatus)	resident
Willet (Catoptrophorus semipalmatus)	resident
Ruddy turnstone (Arenaria interpres)	winter
Red knot (Calidris canutus)	winter
Sanderling (Calidris alba)	winter
Semipalmated sandpiper (Calidris pusilla)	spring, fall
Western sandpiper (Calidris mauri)	winter
Least sandpiper (Calidris minutilla)	winter
Purple sandpiper (Calidris maritima)	winter
Dunlin (Calidris alpina)	winter
Boat-tailed grackle (Quiscalus major)	resident
Fish crow (Corvus ossifragus)	resident
Aerial-searching birds	
Laughing gull (Larus atricilla)	resident
Ring-billed gull (Larus delawarensis)	winter
Herring gull (Larus argentatus)	resident
Great black-backed gull (Larus marinus)	resident
Floating and diving water birds	
Common loon (Gavia immer)	winter
Horned grebe (Podiceps auritus)	winter
Double-crested cormorant (Phalacrocorax auritus)	resident
American wigeon (Anas americana)	winter
Canvasback (Aythya valisineria)	winter
Redhead (Aythya americana)	winter
Ring-necked duck (Aythya collaris)	winter
Greater scaup (Aythya marila)	winter
Lesser Scaup (Aythya affinis)	winter
Oldsquaw (Clangula hyemalis)	winter
Black scoter (Melanitta nigra)	winter
Surf scoter (Melanitta perspicillata)	winter
White-winged scoter (Melanitta fusca)	winter
Common goldeneye (Bucephala clangula)	winter
Red-breasted merganser (Mergus serrator)	winter
Wading birds	
Great blue heron (Ardea herodias)	resident
Great egret (Casmerodius albus)	resident
Snowy egret (Egretta thula)	resident
Green-backed heron (Butorides striatus)	resident
Black-crowned night heron (Nycticorax nycticorax)	resident
Tricolored heron (Egretta tricolor)	resident

[a]Data for this list were assembled from Pearson et al (1942), Stokes and Shackleton (1968), Zingmark (1978), Farrand (1983a, b), Scott et al. (1983), and observations of C. Marsh (University of South Carolina, Coastal Carolina College, Conway, SC), J. Parnell (University of North Carolina, Wilmington, Wilmington, NC), and W. Hon (University of Georgia, Marine Extension Service, Savannah, GA).

CHAPTER 4. ECOLOGICAL PATTERNS AND PROCESSES

This chapter discusses the ecological processes that determine the distribution and abundance of flora and fauna associated with rubble structures in the South Atlantic Bight. In general, we restrict our attention here to waters of relatively high salinity, characterized by predominately marine organisms. In several cases, the processes organizing these communities have not been intensively studied on rubble structures, and we must, therefore, infer their importance from studies conducted in other similar habitats. In this chapter, we outline our general conceptual framework and then concentrate on the organization of intertidal communities, sunlit, subtidal communities (which tend to be dominated by seaweeds), and shaded, subtidal communities (which tend to be dominated by benthic animals). We also discuss the effects of indirect, complex interactions among organisms since these interactions are probably more important than has been generally appreciated.

4.1 CONCEPTUAL FRAMEWORK

In addition to the seasonal temperature effects discussed previously, the two major physical gradients affecting the plant and animal communities of rubble structures are tidal level and availability of sunlight.

The animal communities in particular are well segregated by tidal level for reasons discussed by Jackson (1977). In the intertidal zone solitary sessile animals dominate. These animals usually possess hard external coverings (e.g., shells) which confer superior resistance to the harsher physical conditions experienced when exposed during low tide. Subtidally, colonial animals are more abundant because they have indeterminate, vegetative growth and are less susceptible to overgrowth and grazing. Solitary animals survive subtidally through morphological or behavioral attributes (large size, aggregative behavior) which protect them in competition with colonial animals and from subtidal predators.

Jackson (1977) has also argued that when light is sufficient and all else is equal, colonial animals lose in competition with plants. This is because many plants, like colonial animals, have characteristics that are important in competition (e.g., asexual reproduction and indeterminate growth). Additionally, with adequate light, plants have a further advantage in that they can photosynthetically derive energy for growth and reproduction. In contrast, colonial animals must depend on external food sources. Therefore, seaweeds generally dominate shallow sunlit habitats, and colonial animals generally dominate deeper, darker water and shaded habitats beneath docks and bridges.

Wave action appears less important than tidal level and sunlight, but some organisms, for example the oyster _Crassostrea virginica_, are intolerant of the higher wave action of the open coast (Ortega 1981).

4.2 ORGANIZATION OF INTERTIDAL COMMUNITIES

In spite of the paucity of experimental studies, it is likely that the organization of the invertebrate community on rubble structures is by processes similar to those operating in other rocky intertidal communities (Connell 1972; Menge 1976). On exposed shores, the upper limits of blue-green

algae, barnacles, and mussels are probably controlled by physical factors (e.g. Van Dolah et al. 1984). Chthamalus fragilis is probably restricted to the upper levels of the barnacle zone through competition with larger, faster growing Balanus spp. (Wethey 1983, 1984). Similarly, the lower distributional limit of barnacles is probably set by competition with the mussel Brachidontes exustus since predation on barnacles in the intertidal is minimal (Ortega 1981; Van Dolah et al. 1984). The lower limit of the mussel beds at mean low water (Figure 5) is probably a result of predation by the starfish Asterias forbesii, the sheepshead, (Van Dolah et al. 1984), and the Atlantic oyster drill (Wood 1968). Experimental studies have shown that oyster abundance on exposed jetties is low because exposure to heavy wave action restricts growth and survival and because oysters are outcompeted by the mussel Brachidontes exustus (Ortega 1981).

In protected waters it is also likely that the upper limits of each zone are determined by physical factors while the lower limits are determined by biological factors. Again, Chthamalus fragilis is probably excluded from lower levels through competition with the larger Balanus spp. (e.g. Wethey 1984). Brachidontes exustus is absent from protected waters and Ortega (1981) has shown that oysters competitively exclude barnacles from the oyster zone. In waters of relatively high salinity there is an abrupt end to the oyster zone at mean low water (Wells 1961). This is probably a result of several biological processes, including predation by oyster drills, Urosalpinx cinerea (Chestnut and Fahy 1953) and Thais floridana (Wells and Gray 1960), and shell erosion by the boring sponge Cliona celata (Lunz 1943). Oysters are found subtidally only where low salinity excludes these other species (Wells 1961).

Physical and biological disturbances can cause considerable changes in the abundance of organisms in each zone. For example, near Beaufort, NC, Brachidontes exustus was absent from pilings on the open beach from May through August 1977 (Ortega 1981). Abundance increased to nearly 100% cover in September 1977, remained high until February 1978, and decreased again to near 0% after March. Mortality seemed to be a direct result of wave action on mussels which had increased in size during a winter of growth. It is possible that the wooden substrate provided a less secure attachment site than the granitic rock of which jetties are usually made. However, similar changes in the abundance of mussels were observed on jetties at Murrells Inlet, SC, by Van Dolah et al. (1984), where mortality was a result of winter feeding by ruddy turnstones and gulls.

The intertidal community of invertebrates is resilient (Holling 1973); the general pattern of zonation is restored by recruitment within a year or two after experimental clearing (Ortega 1981) or predation by birds on mussels (Van Dolah et al. 1984).

Although experimental data are lacking, the most likely factors affecting the biomass and species composition of intertidal algal communities on jetties in the South Atlantic Bight are desiccation during low tides and grazing by fishes during high tides. Green algae in the genera Ulva, Enteromorpha, Cladophora, Ulothrix, Chaetomorpha, and Bryopsis and red algae in the genera Gelidium, Erythrotrichia, and Audouinella are commonly among the more abundant seaweeds in the intertidal zone (Williams 1949; Kapraun and Zechman 1982). Feeding preference and gut content studies show these algae to be preferred or heavily used by omnivorous fishes common to the bight. Ogburn (1984) noted that sheepshead tended to feed in the intertidal zone during periods of high tide and that more than 70% of the algae and invertebrates in their stomachs occurred primarily in the intertidal zone at her study site. Hay (1986) documented some of the effects of jetty fishes on patterns of seaweed distribution. Palatable seaweeds like Ulva and Enteromorpha were almost completely excluded from subtidal habitats during warm periods of the year when fishes were common. During cold seasons when fishes were rare, Ulva and Enteromorpha were common in subtidal areas.

Intertidal habitats on rubble structures may serve as partial refuges for palatable algal species that are seasonally eaten to extinction in subtidal habitats by herbivorous fishes (e.g., Hay 1981c, 1984a, 1985; Hatcher and Larkum 1983). Since seaweed productivity in subtidal communities is often much less than in intertidal communities, the effects of herbivory on seaweeds can be much greater in the subtidal zone (Hay 1981c; Hatcher and Larkum 1983). This occurs because productivity often decreases rapidly with depth due to decreasing light and turbulence, which provides nutrients by breaking down diffusion gradients around the algal thallus. Thus, the proportion of net production lost to grazers can be greater in deeper than in shallower waters even if absolute grazing rates are equal. As an example, Vine (1974) and Hay (1981b) found that seaweed production was 27 to over 400 times greater at 2 to 3 m deep than at 13 to 20 m deep on tropical reefs. Thus, if herbivores removed equal amounts of plant material from deep and shallow sites, the effects on the deep habitat plants would be greater since losses would be a larger portion of net growth and take longer to replace. This pattern is compounded by the fact that seaweeds in deeper areas are always available to herbivorous fishes while those in shallower areas periodically escape fishes during low tides and periods of turbulent seas. The effects of herbivorous fishes are discussed at greater length in the following section on the organization of sunlit, subtidal communities.

The effects of other herbivores on intertidal communities have not been studied. The most common sea urchin, Arbacia punctulata, is very prone to desiccation and appears to have little impact in intertidal communities. It is possible that herbivorous amphipods, isopods, or polychaetes could graze intertidal algae and avoid desiccation by sheltering in the bases of algal turfs during low tide. Some of these small mesograzers consume macroalgae (Glynn 1965; Martin 1966; Greze 1968; Nicotri 1977, 1980; Zimmerman et al. 1979; Lewis and Kensley 1982; Norton and Benson 1983; D'Antonio 1985; Gunnill 1985; Hay et al. 1987, 1988), but their effects in the intertidal zone along this coast have not been studied. Herbivorous gastropods have been shown to have a substantial impact on intertidal algal communities in New England and elsewhere (see the review by Hawkins and Hartnoll 1983), but their effects on intertidal hard substrates in the bight have not been studied.

Competition has been demonstrated to play a substantial role in the organization of intertidal algal communities in New England and on the west coast of the United States (Dayton 1971, 1975; Lubchenco 1978, 1980; and others). Descriptive studies of algal seasonality and zonation on jetties in the bight have suggested that competition among seaweeds, and between seaweeds and invertebrates is important in determining community organization in the intertidal zone (Williams 1949; Kapraun and Zechman 1982). However, no experimental evidence is available to either support or refute these contentions.

4.3 ORGANIZATION OF SUNLIT, SUBTIDAL COMMUNITIES

In the shallow subtidal zone, seaweeds tend to be the dominant members of the sessile community. In the one location where succession has been studied, the algal community appeared to be the result of a 3-year-successional process (Van Dolah et al. 1984). Van Dolah and coworkers found that the mussel Brachidontes exustus dominated the subtidal zone in the first year after construction of the jetties at Murrells Inlet. Predation by the starfish Asterias forbesii, and sheepshead appeared to result in the replacement of mussels by hydroids, bryozoans, and tunicates after the first year. These groups in turn were replaced by red and green algae by the third year. This successional process was not entirely predictable; it was observed only on the north jetty. B. exustus dominated the subtidal zone on the south jetty for the two years that it was studied (Van Dolah et al. 1984). However, B. exustus is largely absent from the subtidal zone of jetties in North Carolina (J. Sutherland and M. Hay; pers. obser.). It is likely that mussels are limited to the intertidal zone by predation. The

endpoint of succession appears to be the brown alga, Sargassum filipendula.

No experimental studies have unambiguously demonstrated the importance of the various physical factors that affect the organization of sunlit, subtidal communities in the South Atlantic Bight. However, the large annual changes in water temperature that occur throughout this region clearly have major direct and indirect effects on benthic community structure. Changes in water temperature appear to be directly responsible for the large-scale migration of most fishes from inshore waters in the winter and for their return in the spring. These migrations probably have a substantial effect on energy transfer from inshore to offshore habitats and on inshore and offshore prey populations. As outlined in previous chapters, temperature changes also have major effects on seaweed and invertebrate populations. Some of these organisms must reinvade rubble structures each year, while others have evolved mechanisms for "over-wintering" as resting stages.

Wave action also changes seasonally, and winter storms, or large waves generated in other seasons, can have a substantial impact on subtidal communities. Evidence of this can be seen in the large mass of subtidal organisms occasionally deposited on beaches in the South Atlantic Bight. Since much of the bight is devoid of hard substrate in shallow water, waves may have more impact on rubble structures than on natural hard substrate habitats, which are usually deeper. Waves also increase sand scour and turbidity. Both of these factors should significantly affect benthic community structure by killing, slowing growth, or decreasing reproduction of benthic flora and fauna. Sedimentation and scour might be particularly damaging to newly settled juveniles.

The effects of competition on the organization of sunlit, subtidal communities have rarely been addressed in the South Atlantic Bight. However, experiments have been conducted in hard substrate communities at a depth of 20 m on the Continental Shelf off North Carolina (Peckol and Searles 1983). These experiments indicated that seasonal patterns of recruitment and physical disturbance interacted with competitors and consumers to affect the distribution and abundance of both seaweed and benthic invertebrate populations. When settling plates were in cages that excluded large consumers, competition for space occurred. However, community development was dependent upon season of submergence and upon the seasonal growth and recruitment characteristics of the species involved. In this deep and often poorly lit habitat, it appeared that barnacles would have been the competitive dominants had they not been selectively consumed.

Richardson (1978) conducted a similar study at a depth of 1.5 m below low tide level on the jetty at Radio Island, NC. In his cages, mucous/sand-tube building polychaetes dominated, bivalves and serpulid polychaetes increased, and barnacles and leafy algae decreased in abundance compared to their abundance on plates in open-sided control cages. Some of these changes were interpreted as being a consequence of competition on the caged plates. However, unoccupied space remained at about 50% on plates in the closed cages and it is doubtful that competition caused the reduction in barnacles and leafy algae. Both amphipods and polychaetes along the North Carolina coast have recently been demonstrated to be capable of consuming significant quantities of larger organisms (Hay et al. 1987, 1988). A build-up of these organisms in the cages of both of the above mentioned studies could have significantly affected their results (Brawley and Adey 1981a, b). Since amphipods and polychaetes are common prey of many fishes (Table 2), their increased abundance in fish exclosures seems likely.

Both field and microcosm experiments using seaweeds from jetties in North Carolina demonstrate that seaweeds in close association with larger, overstory algae like Sargassum, experience decreased growth rates due to competition (Hay 1986; Pfister 1987). The consequences of this for community organization have not been adequately evaluated. Given the large role of competition for space, light, and nutrients in other seaweed-dominated communities (Pearse and Hines 1979; Dayton 1975; Kastendiek 1982; Reed and Foster

1984; Santelices and Ojeda 1984), the importance of competition in structuring sunlit, benthic communities in the South Atlantic Bight deserves more attention.

Competition among fishes in the South Atlantic Bight has not been studied, but given the high degree of diet overlap among many fishes on jetties (Table 2) and the high densities of these fishes, competition seems likely. If intra-specific competition for food occurs, then the growth of immature fishes should be density dependent. This pattern has been documented on several occasions and is widespread in marine fishes (Anthony 1971; Cushing and Horwood 1977; Leggett 1977; Rauck and Zijlstra 1978; Jones 1984a, b). However, the importance of interspecific competition in juvenile stages of temperate reef fishes has not been investigated.

For the many juveniles that use rubble structures and estuaries as nurseries, competition from abundant omnivorous fishes, like pinfish and spottail pinfish, could be particularly acute. In shallow habitats along portions of the bight, pinfish and spottail pinfish may comprise more than 50% of the total fish standing stock during the summer and fall. This is also the time when feeding by fishes has reduced the abundance of epifaunal prey to yearly lows (Thayer et al. 1975; Adams 1976a; Nelson 1979, 1980a, b; Darcy 1985a, b). Because the diets of these sparid fishes overlap substantially with the diets of juvenile gag, spot, black sea bass, and others (Adams 1976a; Link 1980), competition between these species and sparids could be particularily important.

One advantage that sparids may have is the ability to feed on plant material when crustacean populations have been depleted. This may allow them to maintain high densities that prevent the recovery of crustaceans and therefore make the area of marginal value for other juvenile fishes. Jones (1984a, b) provides several lines of evidence suggesting that juvenile temperate fishes might be limited by the abundance of epifaunal prey.

Temperate investigations of how herbivorous invertebrates affect algal distribution and the organization of benthic communities in general, have been remarkably fruitful. They have provided both ideas and a data base for many of the generalizations in the current ecological literature (Dayton 1971, 1975; Menge and Sutherland 1976; Lubchenco 1978; Sousa 1979; Paine 1980; Lubchenco and Gaines 1981; Gaines and Lubchenco 1982). The effects of grazing invertebrates on the organization of sunlit, subtidal communities in the South Atlantic Bight, however, are largely uninvestigated. Both Richardson (1978) and Peckol and Searles (1983) demonstrated that exclusion of large consumers could significantly affect benthic prey populations. However, their experiments did not separate the effects of the invertebrates (urchins, large crabs, etc.) from those of the fishes, so the effects of invertebrates alone are unknown.

The most obvious invertebrate herbivores on jetties in the bight are sea urchins. No field experiments have been conducted to assess their effects on community structure. Hay et al. (1986) present some data on the jetty seaweeds that are preferred and avoided by the common sea urchin _Arbacia punctulata_, and on its chemoattraction toward these seaweeds. Some low preference seaweeds like the brown alga _Dictyota dichotoma_ are chemically defended against _Arbacia_ (Hay et al. 1987). Pfister (1987) has also demonstrated that palatable seaweeds gain some protection from grazing _Arbacia_ by being closely associated with unpalatable seaweeds like the brown alga _Sargassum filipendula_. The consequences of these types of interactions are discussed at greater length in the section on complex interactions. Given the significant effects that sea urchins have been shown to have in other benthic marine communities (Lawrence and Sammarco 1982), it is probable that sea urchins, when abundant, significantly affect the organization of communities on rubble structures in the bight.

Other common herbivorous invertebrates include amphipods, isopods, crabs, gastropods, and polychaetes. These can be important herbivores in some habitats (Steneck and Watling 1982; Hawkins and Hartnoll 1983) but little is known of

their effects on subtidal seaweeds in the South Atlantic Bight. Studies of some of these smaller herbivores show that they are rarely resource limited (Zimmerman et al. 1979; Stoner 1980c) but are often strongly affected by their predators (Young et al. 1976; Young and Young 1978; Nelson 1979, 1980a, b, 1981; Stoner 1980a, b; Brawley and Adey 1981a, b; Edgar 1983). They appear to have only limited impact on most seaweeds (Carpenter 1986) because their predators usually keep them well below carrying capacity. However, their potential impact is great. Brawley and Adey (1981a) demonstrated that amphipods could have a large effect on recently established algal communities, and P. Dayton and M. Tegner (Scripps Institution of Oceanography; pers. comm.) have recently observed giant kelp plants (Macrocystis) on the west coast being completely consumed by amphipods when amphipod-consuming fishes were missing from nearshore communities because of events related to the El Niño phenomenon.

Amphipods and polychaetes can also significantly damage seaweeds that are very resistant to fish grazing. Hay and coworkers (Hay et al. 1987, 1988; Paul et al. 1987) have recently shown that seaweeds avoided by omnivorous fishes are often selectively consumed by amphipods and polychaetes (Figure 27) and that the seaweed secondary metabolites that effectively deter feeding by fishes often do not affect, or may even stimulate, feeding by amphipods and polychaetes. They suggest the following reasons for the evolution of this pattern. Because small, relatively sedentary herbivores like tube-building amphipods and polychaetes live on the plants they consume, they should view plants as both foods and living sites. Since large, mobile herbivores like fishes commonly move among, and feed on, many plants, they should view plants primarily as foods and rarely as potential living sites. In the South Atlantic Bight, where fishes that consume plants are also important predators on amphipods and polychaetes (Table 2), seaweeds avoided by fishes should represent safer living sites for small grazers. Thus, small, relatively sedentary herbivores should evolve a preference for seaweeds that are well defended against fishes because if they are living on unpalatable seaweeds

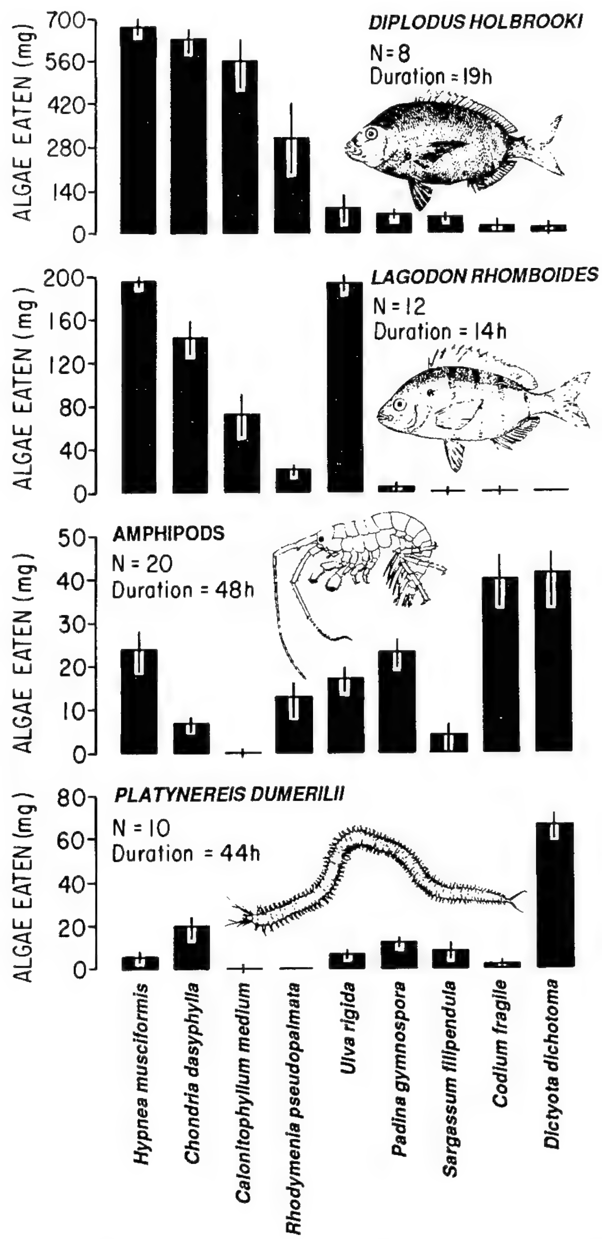


Figure 27. Feeding preferences of two omnivorous fishes and two invertebrate grazers common in the South Atlantic Bight. Lines through the top of each histogram represent ±1 standard error (data from Hay et al. 1987, 1988; M. Hay unpubl.).

they should experience less predation than if they are living on seaweeds preferred by fishes. There are now several documented cases of South Atlantic Bight or Caribbean amphipods and polychaetes

being resistant to seaweed chemical defenses that deter co-occurring fishes. However, there are still no data to suggest that these small grazers sequester the algal metabolites and thereby directly reduce their acceptability as prey to local fishes (Hay et al. 1987). The effects of small grazers on algal community structure clearly warrants increased attention.

Given the large impact that herbivorous invertebrates have been shown to have on temperate algal communities, it is surprising that more attention has not been focused on the effects of temperate herbivorous fishes. These fishes are abundant in the South Atlantic Bight (Figure 26), are very mobile, search visually, and have high metabolic rates relative to co-occurring invertebrate herbivores. It would be surprising therefore if they did not have a large impact on the organization of subtidal community structure. Choat (1982) recently reviewed feeding by fishes in temperate waters and its effects on benthic community structure. He compiled an impressive list of studies that suggest that temperate herbivorous fishes have the potential to affect benthic community structure. However, he concluded that no studies had clearly demonstrated extensive modification of temperate, hard-substrate biota by grazing fishes.

The following families of herbivorous fishes occur in the South Atlantic Bight: Sparidae, Bleniidae, Kyphosidae, Monocanthidae, Mugilidae, and Pomacentridae. Of these, the Sparidae (pinfish, spottail pinfish, and sheepshead) probably have the greatest impact on the community organization of rubble structures because they are often the most abundant fishes in shallow waters (Adams 1976b; Darcy 1985a, b; Hay 1986). They also consume large quantities of benthic macrophytes (Carr and Adams 1973; Adams 1976a; Ogburn 1984; Darcy 1985a, b; Lindquist et al. 1985). As an example, Table 4 shows the stomach contents of 21 spottail pinfish collected from the jetty at Radio Island, NC during late summer. Approximately 98% of the dry mass of stomach contents was plant material. Carr and Adams (1973) reported similar data for several size classes of spottail pinfish ranging from 26 to 167 mm; 50% to 90% of the volume of their stomach contents was algae. When offered a variety of common macrophytes in the lab, both pinfish and spottail pinfish showed a strong preference for some species and consumed very little of others (Hay et al. 1987, 1988; and Figure 27). During mid- to late-summer, high preference species such as _Hypnea_ and _Calonitophyllum_ show dramatic declines in abundance as fish numbers and sizes increase. Low preference species such as _Sargassum_, _Padina_, and _Dictyota_ increase or show no change in abundance at this time (M. Hay; pers. obser.).

To assess the potential effects of temperate herbivorous fishes on the organization of subtidal jetty communities, Hay (1986 and work in progress) constructed eight 5,000-L outdoor microcosms that were designed to mimic the nearby jetty at Radio Island, NC. Each microcosm was divided by 1.5 cm plastic mesh into two equal sized parts of 1 m^2 each. The mean wet mass/m^2 of all common algae from the jetty was attached to the bottom and sides of each partition, and the mean field density of each common herbivorous or omnivorous fish was placed in one portion of each microcosm. Spottail pinfish were stocked at a density of 8/m^2; pinfish and planehead filefish, _Monocanthus hispidus_, were stocked at 1/m^2. Five new cinder blocks were added to each side of each microcosm and were monitored at 2- to 4-week intervals for presence and percent cover of all animal and plant species. The same cinder blocks were monitored without replacement for the entire 4 month study . All microcosms were located immediately adjacent to Bogue Sound and received continuous inputs of unfiltered sound water through an apparatus which also generated waves. The water in the microcosms turned over every 45-90 minutes.

Between the initiation of the experiment in early August and termination in late November, fishes: (1) significantly reduced the abundance and rate of establishment of _Ulva_, _Enteromorpha_, small filamentous algae, and all of the common red seaweeds (_Hypnea_, _Spyridia_, _Chondria_, _Champia_, _Polysiphonia_, _Gracilaria_, and _Neoagardhiella_), (2) significantly increased the abundance of

Table 4. Gut contents of 21 spottail pinfish collected from the jetty at Radio Island, NC, on 1 September 1984. Prey abundance rankings are for the jetty and are subjective. Rare = very difficult or impossible to find. Common = small or isolated individuals can be collected but a kilogram of the material would be difficult or impossible to collect in an hour. Abundant = a kilogram could be collected easily in only a few minutes.

Species	Mean dry mass ± SE (mg)	Frequency of occurrence	Abundance of prey
Small filamentous red algae	50.9 ± 11.0	1.00	rare
Hypnea musciformis	2.7 ± 1.1	0.71	rare to common
Gracilaria tikvahiae	0.4 ± 0.2	0.38	rare to common
Enteromorpha sp.	1.2 ± 0.6	0.76	rare
Ulva sp.	0.5 ± 0.2	0.52	rare
Cladophora sp.	0.2 ± 0.06	0.43	rare
Rhodymenia pseudopalmata	0.1 ± 0.04	0.24	rare to common
Polysiphonia sp.	0.1 ± 0.04	0.19	rare
Bryopsis sp.	0.1 ± 0.05	0.14	rare
Gracilaria verrucosa	0.2 ± 0.02	0.05	rare
Gelidium americanum	0.2 ± 0.02	0.05	common
Calonitophyllum medium	0.2 ± 0.02	0.05	rare
Dictyota dichotoma	0.2 ± 0.02	0.05	abundant
Sargassum filipendula	0.2 ± 0.02	0.05	abundant
Padina gymnospora	0.2 ± 0.02	0.05	abundant
Amphipods	0.1 ± 0.05	0.24	rare
Copepods	0.1 ± 0.05	0.14	?
Other crustaceans	0.6 ± 0.06	0.05	?
Polychaetes	0.1 ± 0.05	0.14	rare
Snails	0.2 ± 0.02	0.05	common
Barnacles	0.1 ± 0.02	0.05	common
Bryozoans	0.1 ± 0.04	0.19	rare
Hydrozoans	0.2 ± 0.02	0.05	rare

unpalatable brown seaweeds such as *Sargassum*, *Padina*, and *Rosenvingea*, (3) significantly decreased the abundance of oysters, ascidians, mussels, arborescent bryozoans, small crustaceans, and worms that lived in soft tubes, (4) either increased or did not affect the abundance of barnacles and worms that constructed hard tubes, and (5) initially decreased the establishment of scallops but later indirectly increased scallop survivorship by preying on crabs. These data strongly suggest that temperate fishes can significantly increase the abundance of relatively unpalatable large brown seaweeds and decrease the abundance of competing red and green seaweeds. Thus, previous suggestions that herbivorous fishes are absent from temperate habitats because these habitats are dominated by relatively unpalatable browns (Bakus 1969; Montgomery and Gerking 1980) may need to be modified if it is found that herbivory by temperate fishes is an important factor in producing and maintaining the dominance of these browns.

Because microcosms are not perfect mimics of the natural system, results from field experiments, when they are conducted, could differ from Hay's results if predators or alternate food sources change the foraging behavior of these herbivorous fishes. However, all available data on the natural history, feeding preferences, and feeding behavior of these fishes under laboratory, microcosm, and field conditions suggest that herbivorous and omnivorous fishes of the South Atlantic Bight have a large effect on the organization of

shallow-water hard-substrate communities (Ogburn 1984; Darcy 1985a, b; Hay 1986; Hay et al. 1987, 1988).

4.4 ORGANIZATION OF SHADED, SUBTIDAL COMMUNITIES

Organisms growing on shaded hard substrates have long been regarded as a source of trouble since they also grow on the bottom of boats and must be periodically scraped off. As a result this assemblage is often referred to as the fouling community. Low light availability generally limits the growth of macroalgae on these substrates, allowing sessile animals to dominate.

The starting point of community development on unoccupied substrate is the recruitment of larvae to that substrate. This process is extremely unpredictable; different patterns of initial development are possible from month to month and from year to year (Mook 1976, 1980; Sutherland and Karlson 1977). Instead of preparing the way for subsequent arrivals, most resident adults strongly inhibit the recruitment and growth of other species (Sutherland 1974, 1977, 1978, 1981; Sutherland and Karlson 1977). This pattern of development appears to conform to what Connell and Slayter (1977) have termed the inhibition model of succession. Species vary in their ability to resist subsequent invasion and larvae vary in their ability to invade assemblages of adult organisms. As a result, the direction and rate of community development are dependent on the order of invasion and are difficult to predict.

The endpoint of community development depends on location and, at times, on the perspective of the observer. Sutherland and Karlson (1977) have argued that near Beaufort, NC, community composition never stops changing and that no climax community is present. As pointed out in previous sections, the winter species assemblage is extremely variable from year to year. However, Sutherland (1981) has also argued that one endpoint is a community dominated by the solitary tunicate _Styela plicata_. This species predictably dominates summer assemblages, inhibits recruitment by other species when present, and reinvades in spring after sloughing off the previous fall. This is analogous to the mussel communities studied by Paine (1966, 1974) and Menge (1976), where patches of mussels are removed by a variety of disturbances, but eventually reinvade. Thus, whether or not a "climax" is present depends on which period is chosen as a reference point and the length of the observation period.

Other shallow water fouling communities near Beaufort in North Carolina "terminate" at different endpoints. In their studies, Sutherland and Karlson worked primarily at the dock of the Duke University Marine Laboratory and the nearby pilings of the railroad bridge across the Beaufort channel. Pilings near the Atlantic Beach bridge in Bogue Sound are dominated by the colonial tunicate _Aplidium constellatum_, which apparently can maintain this competitive dominance for long periods of time. Wells et al. (1964) found the fouling community at Cape Hatteras to be dominated by the colonial tunicate _Botryllus schlosseri_ and various species of sponges.

Near Cape Canaveral in Florida, community development in shallow water ended in assemblages dominated by the tubiculous amphipod _Corophium lacustra_ and several species of _Balanus_, in spite of differences in initial development (Mook 1981). The Florida assemblage was persistent, showing few annual changes in species composition.

On pilings in deeper waters (>2m) near Beaufort, NC, the fouling community is dominated by long-lived forms such as the hydroid _Hydractinia echinata_, the sponge _Xestospongia halichondroides_ and the anemone _Diadumene leucolena_ (Karlson 1978). These species are resistant to grazing by the sea urchin _Arbacia punctulata_, which removes other less resistant forms. Grazer resistant forms tend to recruit at very low intensities, but gradually come to dominate through vegetative growth (or binary fission in anemones). In the presence of _A. punctulata_, these grazer resistant endpoints would presumably be observed regardless of differences in initial development. Indeed, Karlson (1978)

documented enhanced recruitment and vegetative growth of H. echinata in the presence of A. punctulata.

A north-south gradient in the intensity of fish predation on fouling organisms may be present. Near Beaufort, fish are only occasionally important predators and have little to do with the eventual endpoint of community development (Sutherland 1974). Fish can remove small individuals of the tunicate Styela plicata, when they settle on open substrate. However, juveniles of this tunicate commonly find refuges at the base of erect colonies of hydroids and bryozoans, and adults predictably dominate summer assemblages. Near Cape Canaveral, S. plicata is predictably removed from shallow water assemblages by sheepshead. This tunicate dominates only when substrates are experimentally isolated from fish predators (Mook 1981).

4.5 COMPLEX INTERACTIONS

Experimental marine ecologists have been impressively successful in documenting how competition, predation, and physical disturbances affect community structure (Paine 1966; Dayton 1971, 1975; Sutherland 1974; Connell 1975, 1978; Lubchenco 1978; Sousa 1979; Ayling 1981; Hay 1981b; Hixon and Brostoff 1983; Dethier 1984). The best of these studies have also investigated the interactions among the various factors. However, the obvious success achieved by studies focusing primarily on competition, predation, or physical disturbances may have caused ecologists to overlook the importance of more complex, and often indirect, interactions. These interactions can be counter intuitive (i.e. one competitor is dependent on another), and thus are easy to overlook. However, in some cases they may have a major impact on how communities function (Dethier and Duggins 1984; Hay 1986). Two examples of complex interactions that do, or may, occur on jetties in the South Atlantic Bight are described here.

On jetties in the bight, palatable seaweeds can gain significant protection from herbivorous fishes by associating with abundant competitors that are less palatable to these fishes. In fact, when herbivorous fishes are present, palatable seaweeds are completely dependent upon their unpalatable competitors to provide microsites of reduced herbivory that prevent fishes from causing their local extinction. When fishes are excluded, however, the growth rate of palatable species can be severely decreased (by more than 80%) by their association with unpalatable ones (Hay 1986). For these palatable seaweeds, the costs of being associated with an unpalatable competitor are much less than the costs of increased consumption in the absence of that competitor. For the North Carolina jetty community where this interaction was studied, it appeared that removing the dominant (unpalatable) seaweed competitor from the system would cause a decrease, instead of an increase, in the abundance of co-occurring (palatable) competitors (Hay 1986). More recent investigations (Pfister 1987) have shown that these unexpected interactions between competing seaweeds have similar effects on both foraging fishes and sea urchins.

Although there are no rigorous studies of the recruitment of juvenile fishes to jetties or reefs in the South Atlantic Bight, a New Zealand study (Jones 1984a, b) may be instructive for its information on the ecology of a temperate reef fish and for its illustration of complex ecological interactions. Jones' study, as well as extensive work on tropical reefs, suggests that the spatial and temporal changes in distribution and abundance of many species result primarily from patterns of juvenile recruitment (Sale 1980; Williams 1980; Williams and Sale 1981; Doherty 1982, 1983a, b). Jones (1984a, b) showed experimentally that seaweed abundance was critically important in the recruitment of juvenile fish because it provided both cover and food in the form of epifaunal crustaceans. When recruitment was monitored over a wide range of reef habitats, juvenile recruitment at a site was shown to be significantly correlated with algal abundance. Additionally, when seaweeds were removed from some reef areas, recruitment on those areas decreased by 87% compared with nearby controls. When algal abundance was experimentally increased by removing herbivorous sea

urchins, recruitment of juvenile fishes increased approximately sixfold.

The potential interactions between herbivorous sea urchins, seaweeds, and juvenile reef fishes may be of particular interest in heavily fished areas of the South Atlantic Bight since it appears that urchins occur in unusually high abundance primarily in areas that have been heavily fished by people (Estes and Palmisano 1974; Estes et al. 1978; Simenstad et al. 1978; Hay 1984b). On some reefs in the bight, urchins may occur at densities of $>30/m^2$. On jetties near Beaufort, NC, urchin density ranges from <1 to $10/m^2$. Predatory fishes on temperate and tropical reefs have been shown to affect sea urchin distribution, size frequency, and abundance (Tegner and Dayton 1977, 1981; Bernstein et al. 1981; Cowen 1983; Hoffman and Robertson 1983), as well as behavioral patterns, foraging range, and diet breadth (Nelson and Vance 1979; Vance and Schmitt 1979; Carpenter 1984). Studies from both the east and west coasts of North America, as well as the Caribbean, have strongly suggested that human removal of urchin predators indirectly results in unusually high urchin densities and thus the loss of algal cover upon which many other organisms may depend (Estes and Palmisano 1974; Breen and Mann 1976; Estes et al. 1978; Simenstad et al. 1978; Hay 1984b). This could result in longterm suppression of some reef fishes.

CHAPTER 5. MANAGEMENT CONSIDERATIONS

Rubble structures are constructed as part of a management strategy to slow coastal erosion and/or inlet migration. They are designed to solve a local problem, but they almost always have broader impacts on the coastal environment. These impacts are the major focus of this chapter. In the Atlantic Bight, rubble structures represent a unique habitat in otherwise distinctly different surroundings. They can attract large numbers of fishes, but on a regional scale, rubble structures have very little impact on fish and wildlife population sizes or distributions. There are, however, some very localized benefits of jetties to people who fish and to other recreational enthusiasts. These are discussed at the end of the chapter.

5.1 SHORELINE EVOLUTION

In the South Atlantic Bight most rubble structures are installed on barrier islands. To understand the effects that jetties and groins have on these islands it is necessary to understand the dynamics of the interaction between the land and the sea.

The fact of overriding importance is that the level of the sea is rising. Some 15,000-18,000 years ago (at the end of the last ice age) sea level was as much as 100 m lower than at present because of the amount of water tied up in glacial icecaps (Figure 28). As the glaciers melted, sea level rose quite rapidly until about 5,000 years ago. Since then, although the rate of rise has slowed, it continues at about 0.3 m a century (Pilkey et al. 1980). Experts expect this rate of rise may accelerate. The National Academy of Science has warned that the burning of fossil fuels and other activities have resulted in the presence of extra carbon dioxide and other "greenhouse gases" in the atmosphere. The resulting "greenhouse effect" causes the atmosphere to retain

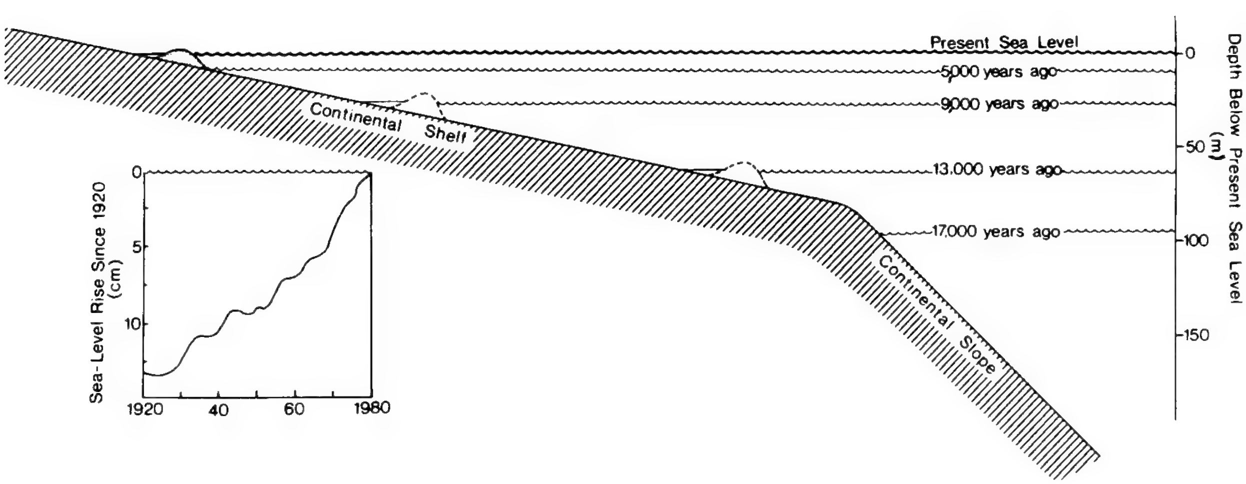


Figure 28. The sea-level rise during the past 17,000 years (from Pilkey et al. 1984).

heat, which increases the melting of the polar ice caps and raises sea level.

As sea level rises, the barrier island-sound system migrates up the Continental Shelf. This process has been operating for the last several thousand years and continues today. The front side of an island is moved backwards by erosion. The back side of the island grows by two processes (Neal et al. 1984). Storm driven waves can carry sand from the beach across the island to the back side in a process known as overwash (Godfrey and Godfrey 1977; Knutson and Finkelstein 1987). In essence, islands migrate by rolling over on themselves like a tank tread. Secondly, storms often form inlets, new passageways between the sound and the ocean. Tidal currents often carry large quantities of sand through these inlets into the sound, forming a tidal delta much thicker than the original island. Longshore currents cause these inlets to migrate, and as they do the island is thickened over the distance of the migration. This process continues as long as the inlet is open. Overwash areas and tidal deltas become stabilized with vegetation and a new sound-side border to the island is formed.

The distance a barrier island migrates with a given rise in sea level is a function of the slope of the Continental Shelf. In much of the South Atlantic Bight the slope is so gradual that a 0.3 m rise in sea level produces a landward migration of the barrier island-sound system of from 30 to 300 m (Pilkey et al. 1975, 1980). This means that current rates of sea level rise translate into a landward migration of 0.3 to 30 m per year. This migration is what beach engineers call erosion.

The size and shape of barrier islands depend on the relative magnitude of tidal and wave energies (Nummedal et al. 1977). The difference in the forms of a tide-dominated and a wave-dominated coastline reflects the ability of the tidal currents to transport sediments through inlets, versus the ability of wave-generated longshore currents to transport sediments along the coast. Along wave-dominated coasts, the longshore currents produce long, continuous barrier islands with small ebb-tidal deltas (sand bodies seaward of inlets) because waves rapidly disperse the sediments. Sediments carried landward into inlets by tidal currents accumulate in large back-barrier flood-tidal deltas because these areas are sheltered from wave dispersal. With an increase in tidal range along tide-dominated coasts, the tidal currents through the inlets increase in strength. Consequently, they can support larger ebb-tidal deltas against the destructive influence of the waves.

In the South Atlantic Bight, barrier islands along the North Carolina coast typify the wave-dominated coastline. The mean tide range is only 0.9-1.2 m (Figure 4). The islands are long, generally narrow, and cut by widely separated tidal inlets with large flood-tidal deltas. They are low in elevation and frequently overwashed (Neal et al. 1984). Islands along the southern South Carolina and Georgia coasts typify a tide-dominated coastline. Here the tidal range is 1.5-2.2 m (Figure 4). The islands are relatively short and stubby and are separated by stable tidal inlets. Large ebb-tidal deltas are associated with all inlets. The islands usually have a well-developed row of sand dunes parallel to the beach that is sufficient to block overwash (Neal et al. 1984).

In the South Atlantic Bight, ocean waves generally hit the coast at an angle which produces longshore currents from north to south. This is the direction in which sand and inlets migrate, especially along wave-dominated coastlines. However, these waves can be refracted by large ebb-tidal deltas, producing south to north currents just south of the inlet. Ebb-tidal deltas may also produce a wave dead zone just south of the inlet. Islands in South Carolina and Georgia that are sufficiently long have the shape of a drumstick as sand is lost (to the ebb-tidal delta of the next inlet) at the south end and sand accumulates at the north. In contrast, islands in North Carolina are of similar width throughout.

For a geologist, beaches extend from the base of the first row of dunes to a depth of 10-15 m offshore. What we usually walk on is only the upper beach.

Beaches are extremely dynamic systems. We have already seen how they respond to rises in sea level and how their size and form is determined by the relative importance of wave and tidal energy. They also respond predictably to the increase in wave energy produced by storms (Figure 29). During a storm, waves take sand from the upper beach or the first dune and transport it to the lower beach. The beach becomes more flattened and storm waves expend their energy over a broader and more level surface. The upper beach can lose a great deal of sand during a storm. Much of it is replenished, however, during fair weather. Sand is pushed shoreward by fair-weather waves or carried in by long-shore transport. The source of sand after storms is the same sand that was on the upper beach prior to the storm.

5.2 SHORELINE ENGINEERING

We have seen that barrier islands in the South Atlantic Bight are extremely dynamic systems. They migrate landward as sea level rises, are moulded by waves and tides, and respond in predictable ways to storms. All of these responses involve the transport of enormous quantities of sand. The engineer's response to this movement, labelled erosion, is to try to stop it and "stabilize" the shore. The most common method is with rubble structures: jetties, groins and seawalls.

Both groins and jetties are successful sand traps. If longshore transport of sand is significant, sand will pile up on the updrift side of the structure. However, this accumulation of sand on the updrift side limits the supply

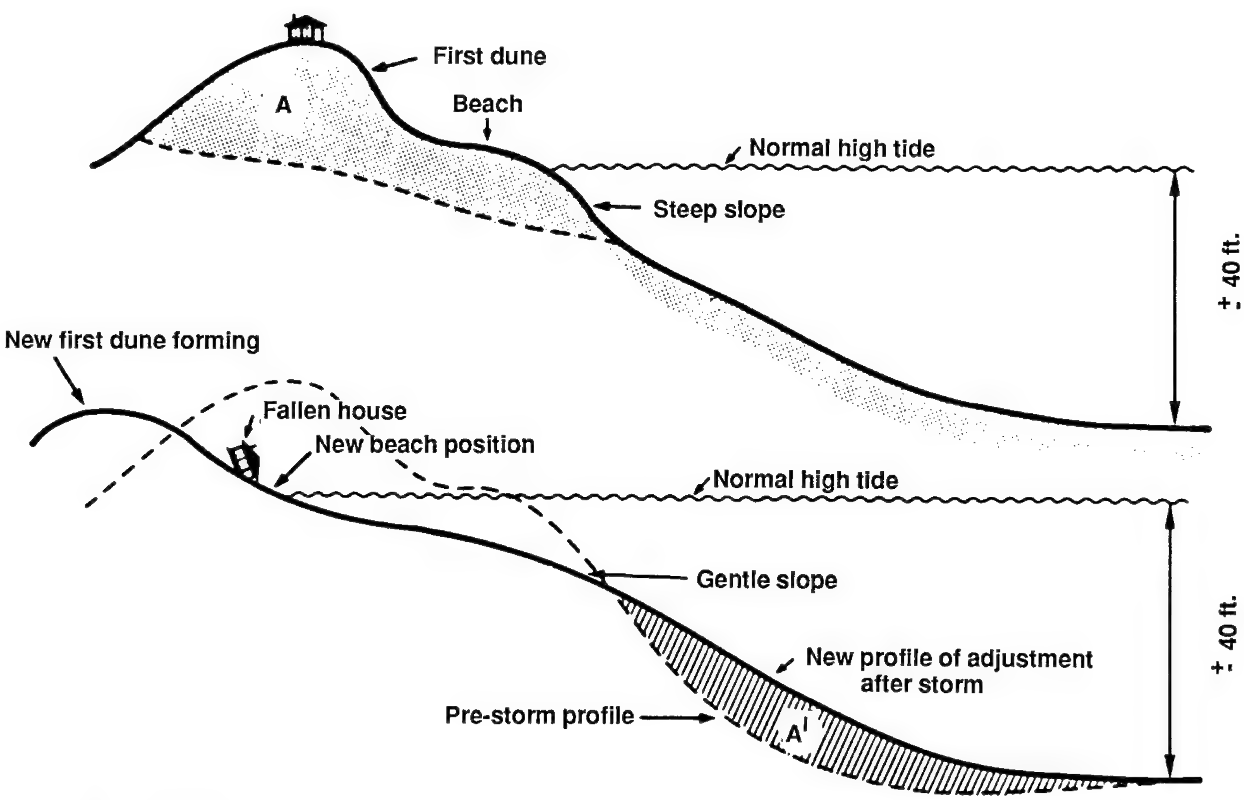


Figure 29. Beach flattening in response to a storm. Shaded area in A' is about equal to shaded area in A. House is not drawn to scale. (From Pilkey et al. 1984).

of sand to beaches on the downdrift side. The result is that these structures actually increase the rate of erosion on downdrift beaches. A classic example of this is represented by the jetties built in 1898 to stabilize the inlet to Charleston Harbor (Neal et al. 1984). Since that time, sand has accreted at Sullivans Island to the north, while Morris Island to the south has been severely eroding. In the mid-1800's, Morris Island had dunes 10-12 m high and a well developed forest of pines and palmettoes. Presently it is a low, rapidly migrating sand flat. The Morris Island Lighthouse, which was approximately 850 m from the shoreline in the late 19th century, now stands 500 m offshore (Figure 30) (Neal et al. 1984).

Recognizing that jetties often cause erosion of "downstream" beaches, newer jetties, such as those at Murrells Inlet, SC, are being built with provisions to move sand from the updrift side of the jetties to the downdrift side. At Murrells Inlet the inner section of the north jetty is a subtidal weir jetty, allowing sand to pass over into a deposition basin (Van Dolah et al. 1984). The design was to allow the basin to be periodically dredged, depositing the sand on the downdrift side of the south jetty.

Seawalls and bulkheads are constructions of last resort (Pilkey et al. 1980). Seawalls reflect wave energy at high tide, increasing the rate of offshore sand transport. This steepens the beach profile, which in turn increases the energy of the waves striking the seawall. Seawalls also increase the intensity of longshore currents, which remove even more sand from in front of the wall. Ultimately the system is self-destructing.

Seawalls and bulkheads also prevent the exchange of sand between the beach and the dunes during storms. The beach cannot

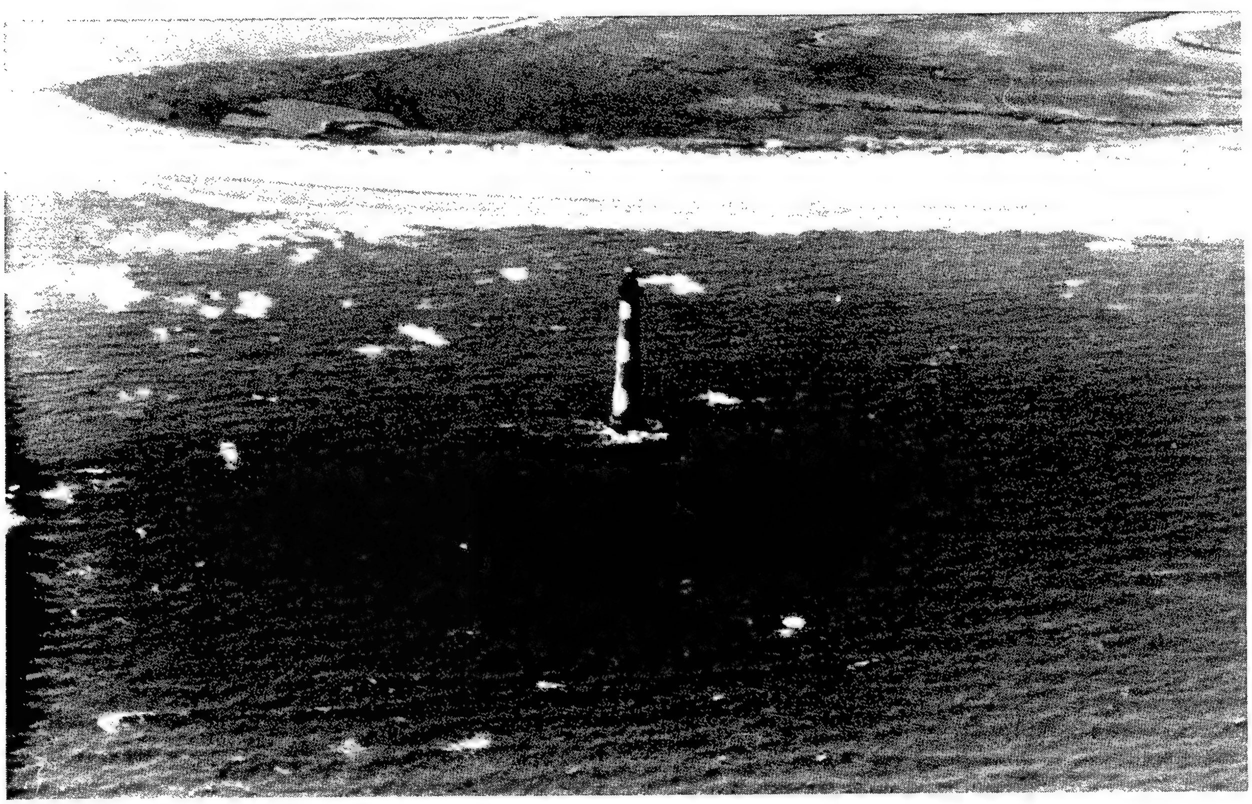


Figure 30. The lighthouse at Morris Island, SC (photo taken by O. Pilkey).

flatten in response to storm generated waves. Instead, the full force of these waves is expended on the structure with the result that it frequently fails. Ultimately, if sea level continues to rise, anything that doesn't migrate shoreward will be destroyed or left at sea like the Morris Island Lighthouse (Figure 30)!

5.3 EFFECTS OF JETTIES ON NEARBY BENTHIC COMMUNITIES

Knot et al. (1984) sampled the macrobenthic communities of the intertidal and nearshore subtidal environments at Murrells Inlet, South Carolina. This was done during the construction of the jetty and once again 5 years later. They found the infaunal community to be dominated by several species of polychaetes (40% of the species and 60% of the individuals), amphipods, and pelecypods. The presence of the jetty appeared to affect the distribution and abundance of only one bivalve and one polychaete. Comparison of species abundance between years and among localities (updrift and downdrift) suggested no widespread impacts attributable to jetty construction.

5.4 JETTIES AS FISHING SITES

Recreational fishing is often concentrated around rubble structures (Figure 31) because of the increased numbers of fishes that occur there. Parker et al. (1979) estimated that an artificial reef constructed off Murrells Inlet, SC, increased fish standing stock in that immediate location by a factor of 1,800. Jetties could have similar consequences and often seem to increase angler densities by similar amounts. Figures 32 and 33 show the seasonal pattern of anglers using the jetties at Murrells Inlet, SC, and the species of fishes caught relative to the types for which they were fishing.

Figure 31. Large jetties like the one at Murrells Inlet, SC, pictured here, provide favored nearshore fishing sites (photo taken by R. Van Dolah).

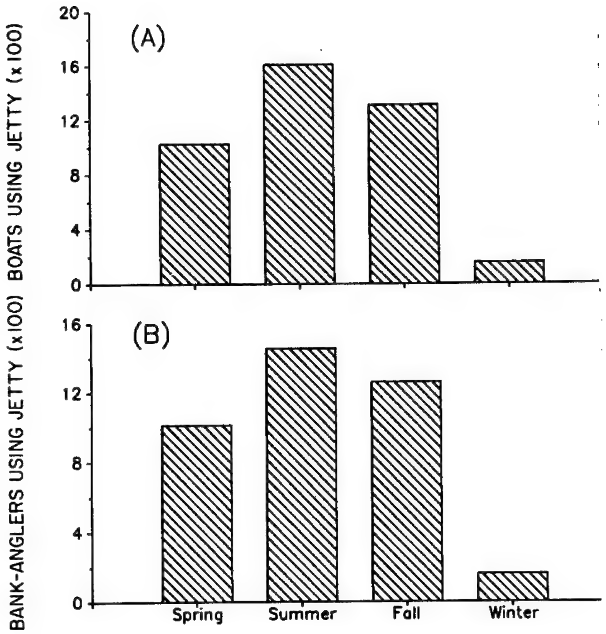


Figure 32. Estimated total number of boats (A) and bank-anglers (B) using the jetties at Murrells Inlet, SC, during different seasons (data from Van Dolah et al. 1986).

5.5 JETTIES AS DIVING SITES

Most of the sport diving industry along the South Atlantic Bight is centered around wreck diving on the Continental Shelf. However, training dives for beginning SCUBA classes and most recreational shore dives take place at jetties since these provide nearshore access to deeper water and allow divers to view higher densities of fishes and benthic organisms. Given the small proportion of the population that dives and the limited number of dives conducted on jetties, jetties do not represent a substantial asset for the sport diving industry. Nonetheless, they provide inexpensive recreational and educational opportunities to individuals that would not otherwise be able to view these reef-like communities.

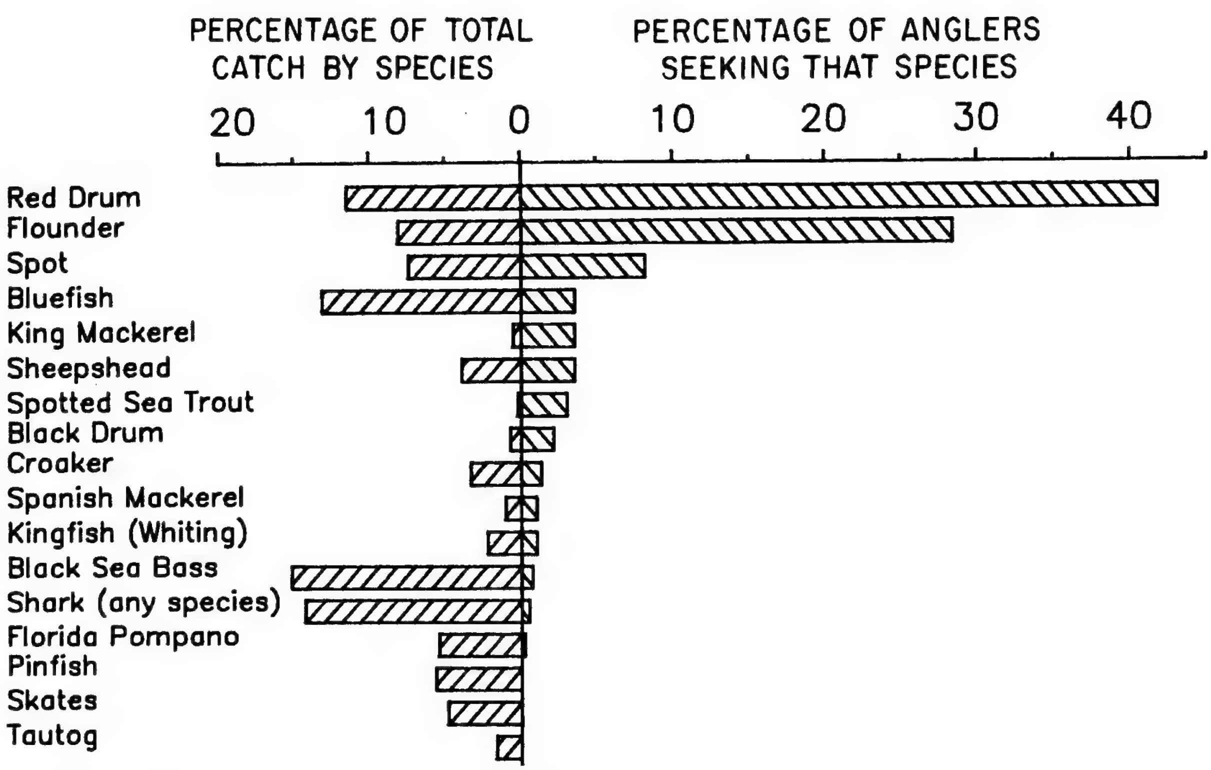


Figure 33. Types of fishes caught compared with types desired by anglers using the jetties at Murrells Inlet, SC (data from Van Dolah et al. 1986).

REFERENCES

Adams, S.M. 1976a. Feeding ecology of eelgrass fish communities. Trans. Am. Fish. Soc. 105:514-519.

Adams, S.M. 1976b. The ecology of Zostera marina (L.) fish communities. II. functional analysis. J. Exp. Mar. Biol. Ecol. 22:293-311.

Amsler, C.D., and R.B. Searles. 1980. Vertical distribution of seaweed spores in a water column offshore of North Carolina. J. Phycol. 16:617-619.

Anthony, V.C. 1971. The density dependence of growth in the Atlantic herring in Maine. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 160:197-205.

Ayling, A.M. 1981. The role of biological disturbance in temperate subtidal encrusting communities. Ecology 62:830-847.

Bakus, G.J. 1964. The effects of fish grazing on invertebrate evolution in shallow tropical waters. Allen Hancock Found. Occas. Pap. 27:1-29.

Bakus, G.J. 1968. Defense mechanisms and ecology of some tropical holothurians. Mar. Biol. 2:23-32.

Bakus, G.J. 1969. Energetics and feeding in shallow marine waters. Int. Rev. Gen. Exp. Zool. 4:275-369.

Bass, R.J., and J.W. Avault, Jr. 1975. Food habits, length-weight relationship, condition factor, and growth of juvenile red drum, Sciaenops ocellatus, in Louisiana. Trans. Am. Fish. Soc. 104:35-45.

Bearden, C.M. 1963. A contribution to the biology of the king whitings genus Menticirrhus of South Carolina. Contrib. Bears Bluff Lab. 38:1-27.

Bengston, D.A. 1984. Resource partitioning by Menidia menidia and Menidia beryllina (Osteichthyes: Atherinidae). Mar. Ecol. Prog. Ser. 18:21-30.

Bernstein, B.B., B.E. Williams, and K.E. Mann. 1981. The role of behavioral responses to predators in modifying urchins' (Strongylocentrotus droebachiensis) destructive grazing and seasonal foraging patterns. Mar. Biol. 63:39-49.

Berrien, P., and D. Finan. 1978. Biological and fisheries data on Spanish mackerel, Scomberomorus maculatus (Mitchill). NMFS Sandy Hook Lab. Tech. Ser. Rep. 9.

Bigelow, H.B., and W.C. Schroeder. 1953. Fishes of the Western North Atlantic. Part 2. Mem. Sears Found. Mar. Res. 15:1-514.

Blair, S.M., and M.O. Hall. 1981. Ten new records of deep water marine algae from Georgia and South Carolina. Northeast Gulf Sci. 4:127-130.

Bohlke, J.E., and C.C.G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publishing. Company, Wynnewood, Pennsylvania. 771 pp.

Bohnsack, J.A., and D.L. Southerland. 1985. Artificial reef research: a review with recommendations for future priorities. Bull. Mar. Sci. 37:11-39.

Boothby, R.N., and J.W. Avault, Jr. 1971. Food habits, length-weight relationship,

a condition factor of the red drum (Sciaenops ocellatus) in southeastern Louisiana. Trans. Am. Fish. Soc. 100: 290-295.

Bozeman, E.L., Jr., and J.M. Dean. 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. Estuaries 3:89-97.

Brawley, S.H., and W.H. Adey. 1981a. The effects of micrograzers on algal community structure in a coral reef microcosm. Mar. Bio. 61:167-177.

Brawley, S.H., and W.H. Adey. 1981b. Micrograzers may affect macroalgal density. Nature 292:177.

Breen, P.A., and K.H. Mann. 1976. Changing lobster abundance and the destruction of kelp beds by sea-urchins. Mar. Biol. 34:137-142.

Buchanan, C.C. 1973. Effects of an artificial habitat on the marine sport fishery and economy of Murrells Inlet, South Carolina. Mar. Fish. Rev. 35:15-22.

Bumpus, D.F. 1973. A description of the circulation on the Continental Shelf of the east coast of the United States. Prog. Oceanogr. 6:111-157.

Caldwell, D.R. 1957. The biology and systematics of the pinfish, Lagodon rhomboides (Linnaeus). Bull. Fla. State Mus. Biol. Sci. 2:77-173.

Carlisle, J.G., Jr., C.H. Turner, and E.E. Ebert. 1964. Artificial habitat in the marine environment. Calif. Dep. Fish. Game Fish Bull. 124:1-93.

Carpenter, R.C. 1984. Predator and population density control of homing behavior in the Caribbean echinoid Diadema antillarum. Mar. Biol. 82:101-108.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56:345-363.

Carr, W.E.S., and C.A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Am. Fish.Soc. 102:511-540.

Chao, L.N., and J.A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull. 75:657-702.

Chapman, R.L. 1971. The macroscopic marine algae of Sapelo Island and other sites on the Georgia coast. Bull. Ga. Acad. Sci. 29:77-89.

Chapman, R.L. 1973. An addition to the macroscopic marine algae of Georgia. The genus Cladophora. Bull. Ga. Acad. Sci. 31:147-150.

Chestnut, A.F., and W.E. Fahy. 1953. Studies on the vertical distribution of setting of oysters in North Carolina. Proc. Gulf Caribb. Fish. Inst. 1952:106-112.

Choat, J.H. 1982. Fish feeding and the structure of benthic communities in temperate waters. Annu. Rev. Ecol. Syst. 13:423-449.

Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. Annu. Rev. Ecol. Syst. 3:169-192.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. Pages 460-490 in M.L. Cody and J.M. Diamond, eds. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Mass.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302-1310.

Connell, J.H., and R.O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-1144.

Cowen, R.K. 1983. The effects of sheephead (Semicossyphus pulcher) predation on red sea urchin

(Strongylocentrotus franciscannus) populations: an experimental analysis. Oecologia (Berl.) 58:249-255.

Currin, B.M., J.P. Seed, and J.M. Miller. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: a comparison of tidal and non-tidal nursery areas. Estuaries 7:451-459.

Cushing, D.H., and J.W. Horwood. 1977. Development of a model of stock and recruitment. Pages 21-35 in Steele, J.H., ed. Fisheries mathematics. Academic Press, London.

Dahlberg, M.D. 1975. Guide to coastal fishes of Georgia and nearby states. University of Georgia Press, Athens. 186 pp.

Dame, R.F. 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. Proc. Nat. Shellfish. Assoc. 69:6-10.

D'Antonio, C. 1985. Epiphytes on the rocky intertidal red alga Rhodomela larix (Turner) C. Agardh: negative effects on the host and food for herbivores? J. Exp. Mar. Biol. Ecol. 86:197- 218.

Darcy, G.H. 1983. Synopsis of biological data on the pigfish, Orthopristis chrysoptera (Pisces:Haemulidae). NOAA Tech. Rep., NMFS Circ. 449.

Darcy, G.H. 1985a. Synopsis of biological data on the pinfish, Lagodon rhomboides (Pisces:Sparidae). NOAA Tech. Rep., NMFS Circ. 23.

Darcy, G.H. 1985b. Synopsis of biological data on the spottail pinfish, Diplodus holbrooki (Pisces:Sparidae). NOAA Tech. Rep., NMFS Circ. 19.

Darnell, R.M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci. Univ. Tex. 5:353-416.

Darnell, R.M. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology 42:553-568.

Davies, J.L. 1964. A morphogenetic approach to world shorelines. Z. Geomorphol. 8:127-142.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45:137-159.

Dethier, M.N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecol. Monogr. 54:99-118.

Dethier, M.N., and D.O. Duggins. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. Am. Nat. 124:205-219.

Diener, R.A., A. Inglis, and G.B. Adams. 1974. Stomach contents of fishes from Clear Lake and tributary waters, a Texas estuarine area. Contrib. Mar. Sci. 18:7-17.

Dixon, P.S. 1965. Perennation, vegetative propagation and algal life histories, with special reference to Asperagopsis and other Rhodophyta. Botanica Gothoburgensia 3:67-74.

Doherty, P.J. 1982. Some effects of density on the juveniles of two species of tropical, territorial damselfishes. J. Exp. Mar. Biol. Ecol. 65:249-261.

Doherty, P.J. 1983a. Tropical territorial damselfishes: is density limited by aggression or recruitment? Ecology 64:176-190.

Doherty, P.J. 1983b. Coral reef fishes: recruitment-limited assemblages?

Proc. Fourth Int. Coral Reef Symp., Philippines 2:465-470.

Earle, L., and H. Humm. 1964. Intertidal zonation of algae in Beaufort Harbor. J. Elisha Mitchell Sci. Soc. 80:78-82.

Edgar, G.J. 1983. The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of ampithoid amphipods among algae. J. Exp. Mar. Biol. Ecol. 70:205-225.

Eiseman, N.J. 1976. Benthic plants of the east Florida Continental Shelf. Annu. Rep. Harbor Branch Found. 1976:A1-A13.

Eiseman, N.J. 1979. Marine algae of the east Florida Continental Shelf. 1. Some new records of Rhodophyta including Scinaia incressata sp. nov. (Nemaliales, Chaaetangiaceae). Phycologia 18:355-361.

Eiseman, N.J., and R.L. Moe. 1981. Maripelta atlantica sp. nov. (Rhodophyta, Rhodomeniales) a new deep-water alga from Florida. J. Phycol. 17:299-308.

Eiseman, N.J., and J.N. Norris. 1981. Dudresnaya patula sp. nov., an unusual deep water red alga from Florida. J. Phycol. 17:186-191.

Estes, J.A., and J.F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058-1060.

Estes, J.A., N.S. Smith, and J.F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59:822-833.

Farrand, J.,Jr., ed. 1983a. The Audubon Society master guide to birding. Vol. 1. Loons to sandpipers. Alfred A. Knopf, New York. 447 pp.

Farrand, J.,Jr., ed. 1983b. The Audubon Society master guide to birding. Vol. 2. Gulls to dippers. Alfred A. Knopf, New York. 397 pp.

Fox, R.S., and E.E. Ruppert. 1985. Shallow-water marine benthic macroinvertebrates of South Carolina. Species identification, community composition, and symbiotic associations. Belle W. Baruch Library in Marine Science, No. 14. University of South Carolina Press, Columbia.

Fulton, R.S., III. 1983. Interactive effects of temperature and predation on an estuarine zooplankton community. J. Exp. Mar. Biol. Ecol. 72:67-81.

Fulton, R.S., III. 1985. Predator-prey relationships in an estuarine littoral copepod community. Ecology 66:21-29.

Gaines, S.D., and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. Annu. Rev. Ecol. Syst. 13:111-138.

Gallaway, B.J., L.R. Martin, R.L. Howard, G.S. Boland, and G.D. Dennis. 1981. Effects on artificial reef and demersal fish and macrocrustacean communities. Pages 237-299 in B.S. Middleitch, ed. Environmental effects of offshore oil production. Plenum Publishing Corp., New York, N.Y.

Gilligan, M.R. (1987). An illustrated field guide to the fishes of Gray's Reef National Sanctuary. NOAA Tech. Rep. OCRM/SPD. In press.

Glynn, P.W. 1965. Community composition, structure, and interrelationships in the marine intertidal Endocladia muricata-Balanus glandula association in Monterey Bay, California. Beaufortia 12:1-198.

Godfrey, P.J., and M.M. Godfrey. 1977. Barrier island ecosystems of Cape Lookout National Seashore and vicinity, North Carolina. Sci. Monogr. 13, Natl. Park Serv., Washington, D.C.

Goff, L.J. 19766. The biology of Harveyella mirabilis (Cryptonemiales, Rhodophyceae). V. Host response to parasite infection. J. Phycol. 12:313 328.

Gosner, K.L. 1979. A field guide to the Atlantic seashore. Houghton Mifflin Co. Boston., 329 pp.

Govoni, J.J., D.E. Hoss, and A.J. Chester. 1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: Brevoortia patronus, Leiostomus xanthurus, and Micropogonias undulatus. Mar. Ecol. Prog. Ser. 413:189-199.

Govoni, J.J., P.B. Ortner, F. Al-Yamant, and L.C. Hill. 1986. Selective feeding of spot, Leiostomus xanthurus, and Atlantic crocker, Micropogonias undulatus, larvae in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 28:175-183.

Grant. G.C. 1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Sci. 3:45-47.

Grant, J.J., K.C. Wilson, A. Grover, and H.A. Togstad. 1982. Early development of Pendleton artificial reef. Mar. Fish. Rev. 44:53-60.

Gray, I.E., and M.J. Cerame-Vivas. 1963. The circulation of surface waters in Raleigh Bay, North Carolina. Limnol. Oceanogr. 8:330-337.

Greze,I.I. 1986. Feeding habits and food requirements of some amphipods in the Black Sea. Mar. Biol. 1:316-321.

Griffin, M.M., and V.J. Henry. 1982. Historical changes in the mean high water shoreline of Georgia 1857-1982. Georgia Dept. Nat. Res., Env. Prot. Div., Georgia Geologic Survey Bull. 98:1-78.

Gunnill, F.C. 1985. Growth, morphology and microherbivore faunas of Pelvetia fastigiata (Phaeophyta, Fucaceae) at La Jolla, California, USA. Bot. Mar. 28:187-199.

Hales, L.S., and M. Van Den Avyle. (1985.) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates. South Atlantic Bight. Spot (Leiostomus xanthurus). U.S. Fish Wildl. Serv. Biol. Rep. 82(11.). U.S. Army Corps of Engineers, TR EL-82-4. In press.

Hall, M.O., and N.J. Eiseman. 1981. The seagrass epiphytes of the Indian River, Florida. I. Species list with descriptions and seasonal references. Bot. Mar. 24:139-146.

Hansen, D.J. 1969. Food, growth, reproduction, and abundance of pinfish, Lagodon rhomboides, and atlantic croaker, Micropogon undulatus, near Pensacola, Florida. Fish. Bull. 68:135-146.

Hansen, M.E., and D.L. Ward. 1986. Response of ebb-tidal deltas to jetty construction. Pages 38-39 in Aubrey, D.G, L. Weishar, D. Duane, and L. Butler, eds. Hydrodynamics and sediment dynamics of tidal inlets. Woods Hole Oceanographic Institution symposium. Woods Hole Oceanographic Institute, U.S. Army Engineer Waterways Experiment Station, Coastal Engineering Research Center.

Harlin, M.M. 1973. Transfer of products between epiphytic marine algae and host plants. J. Phycol. 9:243-248.

Harris, G.P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, model and management. Can. J. Fish. Aquat. Sci. 37:877-900.

Hastings, R.W. 1972. The origin and seasonality of fish fauna on a new jetty in the northeastern Gulf of Mexico. Ph.D. Dissertation. Florida State University, Tallahassee. 124 pp.

Hastings, R.W. 1978. Rock jetty fish fauna as an endangered shore based fishery. Mar. Recreational Fish. 3:29-36.

Hastings, R.W. 1979. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Bull. Fla. State Mus. Biol. Sci. 24:1-122.

Hatcher, B.G., and A.W.D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the

epilithic algal community on a coral reef. J. Exp. Mar. Biol. Ecol. 69:61-84.

Hawkins, S.J., and E. Harkin. 1985. Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. Bot. Mar. 28:223-230.

Hawkins, S.J., and R.G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. 21:195-282.

Hay, M.E. 1981a. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62:739-750.

Hay, M.E. 1981b. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. Am. Nat. 118:520-540.

Hay, M.E. 1981c. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat. Bot. 11:97-109.

Hay, M.E. 1984a. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? Oecologia (Berl.) 64:396-407.

Hay, M.E. 1984b. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65:446-454.

Hay, M.E. 1985. Spatial patterns of herbivore impact and their importance in maintaining algal species richness. Proc. Fifth Int. Coral Reef Congr., Tahiti. 4:29-34.

Hay, M.E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. Am. Nat. 128:617-641.

Hay, M.E., R.R. Lee, R.A. Guieb, and M.M. Bennett. 1986. Food preference and chemotaxis in the sea urchin <u>Arbacia punctulata</u> (Lamarck) Philippi. J. Exp. Mar. Biol. Ecol. 96:147-153.

Hay, M.E., J.E. Duffy, C.A. Pfister, and W. Fenical. 1987. Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology 68:1567-1580.

Hay, M.E., P.E. Renaud, and W. Fenical. 1988. Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia (Berl.). 75:264-252.

Hildebrand, S.F., and L.E. Cable. 1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:383-488.

Hildebrand, S.F., and W.C. Schroeder. 1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:1-366.

Hixon, M.A., and W.N. Brostoff. 1983. Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220:511-513.

Hodson, R.G., J.O. Hackman, and C.R. Bennett. 1981. Food habits of young spots in nursery areas of the Cape Fear River estuary, North Carolina. Trans. Am. Fish. Soc. 110:495-501.

Hoffman, S.G., and D.R. Robertson. 1983. Foraging and reproduction of two Caribbean reef toadfishes (Batrachoididae). Bull. Mar. Sci. 33:919-927.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4:1-23.

Hoss, D.E. 1974. Energy requirements of a population of pinfish <u>Lagodon rhomboides</u> (Linnaeus). Ecology 55:848-855.

Hoyt, W.D. 1920. Marine algae of Beaufort, N.C. and adjacent regions. Bull. Bur. Fish. Wash. 36:367-556.

Humm, H.J. 1952. Notes on the marine algae of Florida. I. The intertidal

rocks at marineland. Stud. Fla. State Univ. 7:17-23.

Humm, H.J. 1969. Distribution of marine algae along the Atlantic coast of North America. Phycologia 7:43-53.

Huntsman, G.R., and C.S. Manooch, III. 1978. Coastal pelagic and reef fishes in the South Atlantic Bight. Pages 97-106 in H. Clepper ed. Proceedings second annual marine recreational fishery symposium, Sport Fish. Inst., Washington D.C.

Hurme, A.K. 1979. Rubble-mound structures as artificial reefs. Proc. Coastal Struct. 79:1042-1051.

Jackson, J.B.C. 1977. Competition on marine, hard substrata: the adaptive significance of solitary and colonial strategies. Am. Nat. 111:743-767.

Johnsgard, P.A. 1981. The plovers, sandpipers, and snipes of the world. University of Nebraska Press, Lincoln. 541 pp.

Johnson, G.F., and L.A. de Wit. 1978. Ecological effects of an artificial island, Rincon Island, Punta Gorda, California. U.S. Army Corps Eng. CERC Misc. Rep. No. 78-3:1-108.

Jones, C.P., and A.J. Mehta. 1978. Ponce de Leon Inlet. Glossary of Inlets Report No. 6. Dep. Coastal Ocean. Eng., Univ. Fla., Fla. Sea Grant Coll.

Jones, G.P. 1984a. Population ecology of the temperate reef fish Pseudolabrus celidotus Bloch and Schneider (Pisces:Labridae). I. Factors influencing recruitment. J. Exp. Mar. Biol. Ecol. 75:257-276.

Jones, G.P. 1984b. Population ecology of the temperate reef fish Pseudolabrus celidotus Bloch and Schneider (Pisces:Labridae). II. Factors influencing adult density. J. Exp. Mar. Biol. Ecol. 75:277-303.

Kapraun, D.F. 1980a. An illustrated guide to the benthic marine algae of coastal North Carolina Vol. I: Rhodophyta. The University of North Carolina Press, Chapel Hill. 206pp.

Kapraun, D.F. 1980b. Floristic affinities of North Carolina inshore benthic marine algae. Phycologia 19:245-252.

Kapraun, D.F. 1984. An illustrated guide to the benthic marine algae of coastal North Carolina Vol. II: Chlorophyta and Phaeophyta. Bibl. Phycol. 58:1-172.

Kapraun, D.F., and F.W. Zechman. 1982. Seasonality and vertical zonation of benthic marine algae on a North Carolina coastal jetty. Bull. Mar. Sci. 32:702-714.

Karlson, R.H. 1978. Predation and space utilization patterns in a marine epifaunal community. J. Exp. Mar. Biol. Ecol. 31:225-239.

Kastendiek, J. 1982. Competitor-mediated coexistence: interactions among three species of benthic macroalgae. J. Exp. Mar. Biol. Ecol. 62:201-210.

Keough, M.J., and H. Chernoff. 1987. Dispersal and population variation in the bryozoan Bugula neritina. Ecology 68:199-210.

Kerr, G.A. 1976. Indian River coastal zone study inventory. Annu. Rep. Harbor Branch Consortium Indian River Coastal Zone Study. 2:1-105.

Kieslich, J.M. 1981. Tidal inlet response to jetty construction. GITI Report 19. U.S. Army Coastal Eng. Res. Cent. Springfield, Va.

Kilby, J.D. 1955. The fishes of two Gulf coastal marsh areas of Florida. Tulane Stud. Zool. 2:173-247.

Kjelson, M.A., D.S. Peters, G.W. Thayer, and G.N. Johnson. 1975. The general feeding ecology of postlarval fishes in the Newport River estuary. Fish. Bull. 73:137-144.

Knott, D.M., R.F. Van Dolah, and D.R. Calder. 1984. Ecological effects of rubble weir jetty construction at Murrells Inlet, South Carolina. Vol. 2:

Changes in macrobenthic communities of sandy beach and nearshore environments. U.S Army Corps Eng. Tech. Rep. EL-84-4, Coastal Eng. Res. Cent., Waterw. Exp. Stn., Vicksburg, Miss. 99 pp.

Knutson, P.L., and K. Finkelstein. 1987. Environmental considerations for dune stabilization projects. U.S. Army Engineer Waterways Experiment Station, Tech. Rep. EL-87-2. 39 pp.

Kobylinski, G.J., and P.F. Sheridan. 1979. Distribution, abundance, feeding and long-term fluctuations of spot, Leiostomus xanthurus, and croaker, Micropogonias undulatus, in Apalachicola Bay, Florida, 1972-1977. Contrib. Mar. Sci. 22:149-161.

Lawrence, J.M., and P.W. Sammarco. 1982. Effects of feeding on the environment: Echinoidea. Pages 499-519 in M. Jangoux and J.M. Lawrence, eds. Echinoderm nutrition. A.A. Balkema Press, Rotterdam, The Netherlands.

Leggett, W.C. 1977. Density dependence, density independence and recruitment in the American shad (Alosa sapidissima) population of the Connecticut River. Pages 3-17 in W. van Winkle, ed. Proceedings of the conference on assessing the effects of power-plant induced mortality on fish populations. Pergamon Press. New York, N.Y.

Lewis, S.M., and B. Kensley. 1982. Notes of the ecology and behavior of Pseudamphithoides incurvaria (Just) (Crustacea, Amphipoda, Amphithoidea). J. Nat. Hist. 16:267-274.

Lindquist, D.G., and R.M. Dillaman. 1986. Trophic morphology of four western Atlantic blennies (Pisces:Blenniidae). Copeia 1986:207-213.

Lindquist, D.G., M.V. Ogburn, W.B. Stanley, H.L. Troutman, and S.M. Pereira. 1985. Fish utilization patterns on rubble-mound jetties in North Carolina. Bull. Mar. Sci. 37:244-251.

Link, G.W., Jr. 1980. Age, growth, reproduction, feeding, and ecological observations on the three species of Centropristis (Pisces:Serranidae) in North Carolina waters. Ph.D. Dissertation. University of North Carolina at Chapel Hill. 277pp.

Lippson, A.J., and R.L. Lippson. 1984. Life in the Chesapeake Bay. Johns Hopkins Univ. Press, Baltimore. 229 pp.

Litaker, W., C.S. Duke, B.E. Kenney, and J. Ramus. (1987). Short-term environmental variability and phytoplankton abundances in a shallow tidal estuary. Part 1: winter and summer. Mar. Biol 96:115-121

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112:23-39.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology 61:333-344.

Lubchenco, J., and S.D. Gaines. 1981. A unified approach to marine-plant herbivore interactions. I. Populations and communities. Annu. Rev. Ecol. Syst. 12:405-437.

Lunz, G.R. 1943. The yield of certain oyster lands in South Carolina. Am. Midl. Nat. 30:806-808.

Manooch, C.S., II. 1984. Fisherman's guide to fishes of the southeastern United States. North Carolina State Museum. Raleigh. 362 pp.

Martin, A.L. 1966. Feeding and digestion in two intertidal gammarids: Marinogammarus obtusatus and M. pirloti. J. Zool. 148:515-552.

Mathieson, A.C., and C.J. Dawes. 1975. Seasonal studies of Florida sublittoral marine algae. Bull. Mar. Sci. 25:46-65.

Maturo, F. J. 1959. Seasonal distribution and settling rates of estuarine bryozoa. Ecology 40:116-127.

McCloskey, L.R. 1970. The dynamics of the community associated with a marine

scleractinian coral. Int. Rev. Gesamten. Hydrobiol. 55:13-81.

McDougall, K.D. 1943. Sessile marine invertebrates of Beaufort, North Carolina. Ecol. Monogr. 13:322-374.

Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. Ecol. Monogr. 46:355-393.

Menge, B.A., and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110:351-359.

Mercer, L.P. 1984a. A biological and fisheries profile of spotted seatrout, Cynoscion nebulosus. Spec. Sci. Rep. No. 40, Proj. SF-13, NMFS.

Mercer, L.P. 1984b. A biological and fisheries profile of the red drum, Sciaenops ocellatus. Special Sci. Rep. No. 41, Proj. SF-13, NMFS.

Merriner, J.V. 1975. Food habits of the weakfish, Cynoscion regalis, in North Carolina waters. Chesapeake Sci. 16:74-76.

Miller, G.C., and W.J. Richards. 1979. Reef fish habitat, faunal assemblages, and factors determining distribution in the South Atlantic Bight. Proc. Gulf Caribb. Fish. Inst. 32:114-130.

Montgomery, W.L. 1977. Diet and gut morphology in fishes with special reference to the monkeyface prickleback Cebidichthys violaceus (Stichaeidae: Blennioidei). Copeia 1977:178-182.

Montgomery, W.L. 1980. The impact of non-selective grazing by the giant blue damselfish Microspathodon dorsalis on algal communities in the Gulf of California, Mexico. Bull. Mar. Sci. 30: 290-303.

Montgomery, W.L., and S.D. Gerking. 1980. Marine macroalgae as food for fishes: an evaluation of potential food quality. Environ. Biol. Fish. 5:143-153.

Mook, D.H. 1976. Studies on fouling invertebrates in the Indian River. 1: seasonality of settlement. Bull. Mar. Sci. 26:610-615.

Mook, D.H. 1980. Seasonal variation in species composition of recently settled fouling communities along an environmental gradient in the Indian River Lagoon, Florida. Estuarine Coastal Mar. Sci. 11:573-581.

Mook, D.H. 1981. Effects of disturbance and initial settlement on fouling community structure. Ecology 62:522-526.

Mook, D.H. 1983a. Indian River fouling organisms, a review. Fla. Sci. 46:162-167.

Mook, D.H. 1983b. Responses of common fouling organisms in the Indian River, Florida, to various predation and disturbance intensities. Estuaries 6:372-379.

Munroe, T.A., and R.A. Lotspeich. 1979. Some life history aspects of the seaboard goby (Gobiosoma ginsburgi) in Rhode Island. Estuaries 2:22-27.

Naughton, S.P., and C.H. Saloman. 1981. Stomach contents of juveniles of king mackerel (Scomberomorus cavalla) and Spanish mackerel (S. maculatus). Northeast Gulf Sci. 5:71-74.

Neal W.J., W.C. Blakeney, Jr., O.H. Pilkey, Jr., and O.H. Pilkey, Sr. 1984. Living with the South Carolina shore. Duke University Press, Durham, North Carolina. 205 pp.

Nelson, B.V., and R.R. Vance. 1979. Diel foraging patterns of the sea urchin Centrostephanus coronatus as a predator avoidance strategy. Mar. Biol. 51:251-258.

Nelson, W.G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J. Exp. Mar. Biol. Ecol. 38:225-245.

Nelson, W.G. 1980a. The biology of eelgrass (Zostera marine L.) amphipods. Crustaceana 39:59-89.

Nelson, W.G. 1980b. A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bull. Mar. Sci. 30:80-89.

Nelson, W.G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar. Biol. Prog. Ser. 5:141-149.

Nicotri, M.E. 1977. The impact of crustacean herbivores on cultured seaweed populations. Aquaculture 12:127-136.

Nicotri, M.E. 1980. Factors involved in herbivore food preference. J. Exp. Mar. Biol. Ecol. 42:13-26.

Norton, T.A., and M.R. Benson. 1983. Ecological interactions between the brown seaweed Sargassum muticum and its associated fauna. Mar. Biol. 75:169-177.

Nummedal, D., G.F. Oertel, D.K. Hubbard, and A.C. Hine. 1977. Tidal inlet variability--Cape Hatteras to Cape Canaveral. Coastal sediments '77. proc. Fifth Symp. WPCO Div. Am. Soc. Civ. Eng. 1977:543-562.

Odum, W.E., and E.J. Heald. 1972. Trophic analysis of an estuarine mangrove community. Bull Mar. Sci. 22:671-738.

Ogburn, M.V. 1984. Feeding ecology and the role of algae in the diet of the sheepshead Archosargus probatocephalus (Pisces: Sparidae) on two North Carolina jetties. M.S. Thesis. University of North Carolina at Wilmington. 68 pp.

Ogden, J.S., and P.S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Environ. Biol. Fish. 3:49-63.

Olla, B.L., A.J. Bejda, and A.D. Martin. 1974. Daily activity, movements, feeding, and seasonal occurrence in the tautog, Tautoga onitis. Fish. Bull. 72:27-35.

Ortega, S. 1981. Environmental stress, competition and dominance of Crassostrea virginica near Beaufort, North Carolina, USA. Mar. Biol. 62:47-56.

Overstreet, R.M., and R.W. Heard. 1978a. Food of the red drum, Sciaenops ocellatus from Mississippi Sound. Gulf Res. Rep. 6:131-135.

Overstreet, R.M., and R.W. Heard. 1978b. Food contents of six commercial fishes from Mississippi Sound. Gulf. Res. Rep. 7:137-149.

Overstreet, R.M., and R.W. Heard. 1982. Food contents of six commercial fishes from Mississippi Sound. Gulf Res. Rept. 7:137-149.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.

Paine, R.T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berl.) 15:93-120.

Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. J. Anim. Ecol. 29: 667-685.

Parchure, T.M. 1982. St. Marys entrance. Glossary of Inlets Report 11. Dep. Coastal Ocean. Eng., Univ. Fla. Fla. Sea Grant Coll. 46 pp.

Parker, R.O., Jr., R.B. Stone, and C.C. Buchanan. 1979. Artificial reefs off Murrells Inlet, South Carolina. Mar. Fish. Rev. 1979:12-24.

Paul, V.J., M.E. Hay, J.E. Duffy, W. Fenical, and K. Gustafson (1987). Chemical defense in the seaweed Ochtodes secundiramea (Montagne) Howe (Rhodophyta): effects of its monoterpenoid components upon diverse coral reef herbivores. J. Exp. Mar.Biol. Ecol. 114:249-260.

Pearse, J.S., and A.H. Hines. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. Mar. Biol. 51:83-91.

Pearson, J.C. 1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.

Pearson, T.G., C.S. Brimley, and H.H. Brimley. 1942. Birds of North Carolina. 2nd ed. Bynum Printing Co., Raleigh. 434 pp.

Peckol, P. 1982. Seasonal occurrence and reproduction of some marine algae of the Continental Shelf, North Carolina. Bot. Mar. 25:185-190.

Peckol, P., and R.B. Searles. 1983. Effects of seasonality and disturbance on the population development in a Carolina Continental Shelf community. Bull. Mar. Sci. 33:67-86.

Peterson, C.H., and N.M. Peterson. 1979. The ecology of intertidal flats of North Carolina: a community profile U.S. Fish and Wildlife Service, Office of Biological Services. FWS/OBS-79/39. 73 pp.

Pfister, C.A. 1987. Associational plant refuges: convergent patterns in terrestrial and marine communities are the result of differing mechanisms. M.S. Thesis. University of North Carolina at Chapel Hill. 39 pp.

Pilkey, O.H.,Jr., O.H. Pilkey,Sr., and R. Turner. 1975. How to live with an island. A handbook to Bogue Banks, North Carolina. North Carolina Department of Natural and Economic Resources, Raleigh. 119 pp.

Pilkey, O.H., Jr., W.J. Neal, O.H.Pilkey, Sr., and S.R. Riggs. 1980. From Currituck to Calabash. Living with North Carolina's barrier islands. Duke University Press, Durham, North Carolina. 245 pp.

Pilkey, O.H., Jr., D.C. Sharma, H.R. Wanless, L.J. Doyle, O.H. Pilkey, Sr. W.J. Neal, and B.L. Gruver. 1984. Living with the East Florida shore. Duke University Press, Durham, North Carolina. 259 pp.

Ramus, J., and M. Venable. 1987. Temporal ammonium patchiness and growth rate in Codium and Ulva (Ulvophyceae). J. Phycol 23:518-523.

Randall, J.E. 1967. Food habitats of reef fishes of the West Indies. Studies in Tropical Oceanography (Miami). 5:665-847.

Randall, J.E., and W.D. Hartman. 1968. Sponge-feeding fishes of the West Indies. Mar. Biol. 1:216-225.

Rauck, G., and J.J. Zijlstra. 1978. On the nursery aspect of the Wadden Sea for some commercial fish species and possible long-term changes. Rapp. P. V. Reun. Cons. Int. Explor. Mer. 172:266-275.

Reed, D.C., and M.S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65:937-948.

Reid, G.K., A. Inglis, and H.D. Hoese. 1956. Summer foods of some fish species in East Bay, Texas. Southwest Nat. 1:100-104.

Richards, S.W. 1976. Age, growth, and food of bluefish (Pomatomus saltatrix) from east-central Long Island sound from July through November 1975. Trans. Amer. Fish. Soc. 105:523-525.

Richards, S.W. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Report to the Bureau of Land Management under Contract No. AA550-CT7-28, June 1979. 546 pp.

Richardson, J.P. 1978. Effects of environmental factors on the life histories and seasonality of some inshore benthic marine algae in North Carolina. Ph.D. Dissertation. University of North Carolina at Chapel Hill. 141 pp.

Richardson, J.P. 1979. Overwintering of Dictyota dichotoma (Phaeophyceae) near its northern distribution limit on the east coast of North America. J. Phycol. 15:22-26.

Richardson, J.P. 1981. Persistence and development of Dasya baillouviana (Gemelin) Montagne (Rhodophyceae,

Dasyaceae) in North Carolina. Phycologia 20:385-391.

Richardson, J.P. 1982. Life history of Bryopsis plumosa (Hudson) Agardh (Chlorophyceae) in North Carolina, USA. Bot. Mar. 25:177-183.

Robins, C.R., G.C. Ray, and J. Douglas. 1986. A field guide to Atlantic coast fishes of North America. Peterson Field Guide Series No.32. Houghton Mifflin Co., Boston. 354 pp.

Roelofs, E.W. 1954. Food studies of young sciaenid fishes, Micropogon and Leiostomus, from North Carolina. Copeia 1954:151-153.

Rosenberg, G., and H.W. Paerl. 1980. Nitrogen fixation by bluegreen algae associated with the siphonous green seaweed Codium decorticatum: effects on ammonium uptake. Mar. Biol. 61:151-158.

Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 18:367-421.

Santelices, B., and F.P. Ojeda. 1984. Effects of canopy removal on the understory algal community structure of coastal forests of Macrocystis pyrifera from southern South America. Mar. Ecol. Prog. Ser. 14:165-173.

Schneider, C.W. 1975. Spatial and temporal distribution of benthic marine algae on the Continental Shelf of the Carolinas. Ph.D. Dissertation. Duke University, Durham, North Carolina. 196 pp.

Schneider, C.W. 1976. Spatial and temporal distribution of benthic marine algae on the Continental Shelf of the Carolinas. Bull. Mar. Sci. 26:133-151.

Schneider, C.W., and R.B. Searles. 1979. Standing crop of benthic seaweeds on the Carolina Continental Shelf. Proc. Int. Seaweed Symp. 9:293-301.

Schwartz, F.J. 1964. Fishes of the Isle of Wight and Assawoman Bays near Ocean City, Maryland. Chesapeake Sci. 5:172-193.

Schwartz, F.J., and B.W. Dutcher. 1963. Age, growth, and food of the oyster toadfish near Solomans, Maryland. Trans. Amer. Fish. Soc. 92:170-173.

Scott, S.L., L.M. Swinson, M.B. Dickinson, and C.H. Howell. 1983. Field guide to the birds of North America. Nat. Geo. Soc., Washington, DC. 463 pp.

Searles, R.B. 1981. Seaweeds from Gray's Reef, Georgia. Northeast Gulf Sci. 5:45-48.

Searles, R.B. 1984. Seaweed biogeography of the mid-Atlantic coast of the United States. Helgol. Meeresunters 38:259-271.

Searles, R.B., M.H. Hommersand, and C.D. Amsler. 1984. The occurrence of Codium fragile subs. tomentosoides and C. taylorii in North Carolina. Bot. Mar. 27:185 187.

Searles, R.B., and C.W. Schneider. 1978. A checklist and bibliography of North Carolina seaweeds. Bot. Mar. 21:99-108.

Searles, R.B., and C.W. Schneider. 1980. Biogeographic affinities of the shallow and deep water benthic marine algae of North Carolina. Bull. Mar. Sci. 30:732-736.

Sears, J.R. 1971. Morphology, systematics and descriptive ecology of the sublittoral benthic marine algae of southern Cape Cod and adjacent islands. Ph.D. Dissertation. University of Massachusetts, Amherst. 273 pp.

Sedberry, G.R., and R.F. Van Dolah. 1984. Demersal fish assemblages associated with hard bottom habitats in the South Atlantic Bight of the U.S.A. Environ. Biol. Fishes 11:241-258.

Sheridan, P.F., and D.L. Trimm. 1983. Summer foods of Texas coastal fishes relative to age and habitat. Fish. Bull. 81:643-647.

Simenstad, C.A., J.A. Estes, and K.W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science 200:403-411.

Smith, S.M., J.G. Hoff, S.P. O'Neil, and M.P. Weinstein. 1984. Community and trophic organization of nekton utilizing shallow marsh habitats, York River, Virginia. Fish. Bull. 82:455-467.

Sousa, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49:227-254.

Spitsbergen, J.M. 1980. Seacoast life. An ecological guide to natural seashore communities in North Carolina. Univ. N.C. Press, Chapel Hill. 112 pp.

Springer, V.G., and K.D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Fla. Board Conserv. Mar. Res. Lab. Prof. Pap. Ser. 1. 104 pp.

Stefansson, U., L.P. Atkinson, and D.F. Bumpus. 1971. Hydographic properties and circulation of the North Carolina shelf and slope waters. Deep Sea Res. 18:383-420.

Steimle, F.W., Jr., and L. Ogren. 1982. Food of fish collected on artificial reefs in the New York Bight and off Charleston, South Carolina. Mar. Fish. Rev. 44:49-52.

Steneck, R.S., and L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Mar. Biol. 68:299-319.

Stephenson, T.A., and A. Stephenson. 1952. Life between tidemarks in North America, Part 2. Northern Florida and the Carolinas. J. Ecol. 40:1-49.

Stephenson, T.A., and A. Stephenson. 1972. Life between tidemarks on rocky shores. W.H. Freeman and Co., San Francisco. 425 pp.

Stickney, R.R., G.L. Taylor, and D.B. White. 1975. Food habits of five species of young southeastern United States estuarine Sciaenidae. Chesapeake Sci. 16:104-114.

Stokes, T., and K. Shackleton. 1968. Birds of the Atlantic Ocean. Macmillan Co., New York. 156 pp.

Stoner, A.W. 1980a. Feeding ecology of Lagodon rhomboides (pisces: Sparidae): variation and functional response. Fish. Bull. 78:337-352.

Stoner, A.W. 1980b. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bull. Mar. Sci. 30:537-551.

Stoner, A.W. 1980c. Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachea Bay, Florida. Cont. Mar. Sci. 23:63-77.

Stoner, A.W., and R.J. Livingston. 1984. Ontogenetic pattern and feeding morphology in sympatric sparid fishes from seagrass meadows. Copeia 1984:174-187.

Sutherland, J.P. 1974. Multiple stable points in natural communities. Am. Nat. 108:859-873.

Sutherland, J.P. 1977. Effect of Shizoporella removal in the fouling community at Beaufort, N.C. Pages 155-189 in B.C. Coull, ed. Ecology of marine benthos. University of South Carolina Press, Columbia.

Sutherland, J.P. 1978. Functional roles of Shizoporella and Styela in the fouling community at Beaufort, North Carolina. Ecology 59:257-264.

Sutherland, J.P. 1981. The fouling community at Beaufort, North Carolina: a study in stability. Am. Nat. 118:499-519.

Sutherland, J.P., and R.H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecol. Monogr. 47:425-446.

Taylor, W.R. 1960. The marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor. 870 pp.

Tegner, M.J., and D.K. Dayton. 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science 196:324-326.

Tegner, M.J., and P.K. Dayton. 1981. Population structure, recruitment and mortality of two sea urchins (Strongylocentrotus franciscanus and S. purpuratus) in a kelp forest. Mar. Ecol. Prog. Ser. 6:223-228.

Thayer, G.W., D.E. Hoss, M.A. Kjelson, W.F. Hettler,Jr., and M.W. La Croix. 1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. Chesapeake Sci. 15:9-16.

Thayer, G.W., S.M. Adams, and M.V. La Croix. 1975. Structural and functional aspects of a recently established Zostera marina community. Estuarine Res. 1:517-540.

Thayer, G.W., W.J. Kenworthy, and M.S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. U.S. Fish. Wildl. Serv. FWS/OBS-84/02. 147 pp.

Turner, C.H., E.E. Ebert, and R.R. Given. 1969. Man-made reef ecology. Calif. Dep. Fish Game Fish Bull. 146:1-221.

U. S. Army Corps of Engineers. 1984. Shore protection manual. 2 Vols. Coastal Engineering Research Center, Department of the Army, Waterways Experiment Station, Vicksburg, Mississippi.

U. S. Department of Commerce. 1987. Tide tables 1987. East Coast of North and South America. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service. 289 pp.

Vance, R.R., and R.J. Schmitt. 1979. The effects of the predator avoidance behaviour of the sea urchin Centrostephanus coronatus on the breadth of its diet. Oecologia (Berl.) 44:21-25.

Van Dolah, R.F., D.M. Knott, and D.R. Calder. 1984. Ecological effects of rubble weir jetty construction at Murrells Inlet, South Carolina; Volume I: Colonization and community development on new jetties. U.S. Army Corps Eng. Tech. Rep. EL-84-4, Coastal Eng. Res. Cent. Waterw. Exp. Stn., Vicksburg, Miss. 143 pp.

Van Dolah, R.F., P.H. Wendt, C.A. Wenner, R.M. Martore, G.R. Sedberry, and C.A. Moore. 1986. Ecological effects of rubble weir jetty construction at Murrells Inlet, South Carolina. Volume III: Community structure and habitat utilization of fishes and crabs associated with the jetties. U.S. Army Corps Eng. Tech. Rep. EL-84-4. Coastal Eng. Res. Cent., Waterw. Exp. Stn., Vicksburg, Miss. 150 pp.

Van Dover, C., and W. Kirby-Smith. 1979. Field guide to common marine invertebrates of Beaufort, NC. Part 1. Gastropods, bivalves, amphipods decapods, and echinoderms. Duke University Marine Laboratory, Beaufort. 78 pp.

Vine, P.J. 1974. The effect of algal grazing and aggressive behavior of the fishes Pomacentrus lividus and Acanthurus sohal on coral reef ecology. Mar. Biol. 24:131-136.

Wang, J.C.S., and E.C. Raney. 1971 Distribution and fluctuations in the fish fauna of the Charlotte Harbor estuary, Florida. Charlotte Harbor Estuarine Study, Mote Marine Laboratory, Sarasota, Florida. 56 pp.

Whalin, R.W., F.E. Camfield, N.E. Parker, R.A. Jachowski, and J.R. Weggel. 1984. Shore protection manual. Vols. 1 and 2. Dept. Army, Waterways Experiment Station, Corps of Engineers, Coastal Engineering Research Center. U.S. Gov. Print. Off., Washington, DC. 597 pp.

Williams, D. M. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). Bull. Mar. Sci. 30:159-170.

Williams, D. M., and P.F. Sale. 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within "One Tree Lagoon", Great Barrier Reef. Mar. Biol. 65:245-253.

Williams, L.G. 1948. Seasonal alterations of marine floras at Cape Lookout, North Carolina. Am. J. Bot. 35:682-695.

Williams, L.G. 1949. Marine algal ecology at Cape Lookout, North Carolina. Bull. Furman Univ. 31:1-21.

Wiseman, D.R. 1978. Benthic marine algae. Pages 23-36 in R.G. Zingmark, ed. An annotated checklist of the biota of the coastal zone of South Carolina. University of South Carolina Press, Columbia.

Wiseman, D.R., and C.W. Schneider. 1976. Investigations of the marine algae of South Carolina. I. New records of Rhodophyta. Rhodora 78:516-524.

Wells, H.W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31:239-266.

Wells, H.W., and I.E. Gray. 1960. Some oceanic subtidal oyster populations. Nautilus 73:139-146.

Wells, H.W., M.J. Wells, and I.E. Gray. 1960. Marine sponges of North Carolina. J. Elisha Mitchell Sci. Soc. 76:200-245.

Wells, H.W., M.J. Wells, and I.E. Gray. 1964. Ecology of sponges in Hatteras Harbor, North Carolina. Ecology 45:752-767.

Wenner, C.A., W.A. Roumillat, and C.W. Waltz. 1986. Contributions to the life history of black seabass, Centropristis striata, off the southeastern United States. Fish. Bull. 84:723-741.

Wethey, D.S. 1983. Geographic limits and local zonation: the barnacles Semibalanus (Balanus) and Chthamalus in New England. Biol. Bull. 165:330-341.

Wethey, D.S. 1984. Sun and shade mediate competition in the barnacles Chthamalus and Semibalanus: a field experiment. Biol. Bull. 167:176-185.

Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod Urosalpinx cinerea (Prosobranchia: Muricidae). Malacologia 6:267-320.

Young, D.K., M.A. Buzas, and M.W. Young. 1976. Species densities of macrobenthos associated with seagrass: a field experimental study of predation. J. Mar. Res. 34:577-592.

Young, D.K., and M.W. Young. 1978. Regulation of species densities of seagrass associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. J. Mar. Res. 36:569-593.

Zimmerman, R., R. Gibson, and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54:41-47.

Zingmark, R.G., ed. 1978. An annotated checklist of the biota of the coastal zone of South Carolina. Univ. South Carolina Press, Columbia. 364 pp.

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REPORT DOCUMENTATION PAGE	1. REPORT NO. Biological Report 85(7.20)	2.	3. Recipient's Accession No.

4. Title and Subtitle The Ecology of Rubble Structures of The South Atlantic Bight: A Community Profile	5. Report Date September, 1988
	6.
7. Author(s) Mark E. Hay[a] and John P. Sutherland[b]	8. Performing Organization Rept. No.
9. Authors' addresses: [a]University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City, NC 28557 [b]Duke University, Marine Laboratory, Beaufort, NC 28516	10. Project/Task/Work Unit No.
	11. Contract(C) or Grant(G) No. (C) (G)
12. Sponsoring Organization Name and Address U.S. Department of the Interior Fish and Wildlife Service National Wetlands Research Center Washington, DC 20240	13. Type of Report & Period Covered
	14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

This community profile provides an introduction to the ecology of the communities living on and around rubble structures in the South Atlantic Bight (Cape Hatteras to Cape Canaveral). The most prominent rubble structures in the bight are jetties built at the entrances to major harbors. After an initial discussion of the various kinds of rubble structures and physical factors that affect the organisms associated with them, the major portion of the text is devoted to the ecology of rubble structure habitats. Community composition, distribution, seasonality, and the recruitment patterns of the major groups of organisms are described. The major physical and biological factors affecting the organization of intertidal, sunlit subtidal, and shaded subtidal communities are presented and the potential effects of complex interactions in structuring these communities are evaluated. The profile concludes with a general review of the effects of rubble structures on nearshore sediment dynamics and shoreline evolution.

17. Document Analysis a. Descriptors

South Atlantic Bight
jetties
groins
rubble structures
hard substrate communities
fouling communities
encrusting organisms
North Carolina
South Carolina
Georgia
northern Florida

b. Identifiers/Open-Ended Terms

Algae
barnacles
anemones
fish

c. COSATI Field/Group

18. Availability Statement	19. Security Class (This Report)	21. No. of Pages
Unlimited distribution	Unclassified	ix + 67
	20. Security Class (This Page) Unclassified	22. Price

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce